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Hydrophytes, Xerophytes and Halophytes and the Production of Alkaloids, Cyanogenetic and Organic Sulphur Compounds

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Electrolyte concentration in the leaf tissue fluid of halophytes is decidedly greater than in that of hydrophytes. Consequently, according to the law of mass action, we might expect to find in halophytes new compounds composed of some of the atoms of the electrolytes. Also in accordance with the law of mass action, these new compounds might occur more frequently, have greater molecular weights, or be found in greater concentration in halophytes than in hydrophytes.

DEFINITIONS

As there are several definitions for hydrophytes, xerophytes and halophytes it might be well to define these terms as they will be used in this paper.

Hydrophytes.—A hydrophyte is defined as a plant that may, under normal conditions, germinate and grow with at least its base in the water and is large enough to be seen with the naked eye (Fassett, 1940). Hydrophytes may comprise entire families as, Pontederiaceae, Podostemaceae, Potamogetonaceae; or entire genera as *Ludwigia*, *Jussieuia*, *Hottonia*; or species of otherwise terrestrial genera as *Ranunculus aquatilis* L., *Lobelia Dortmanna* L., *Bidens Beckii*. Some genera and species are amphibious such as *Elatine*, *Marsilea*, *Ranunculus Flammula*, *Littorella lacustris*, *Polygonum amphibium*. Some genera and species are halophytes, e.g., *Enalus*, *Halophida* and some *Lophotocarpus* species. Some plants are xerophytes at one period of the year and hygrophytic at another (tropophytes), e.g., bulbs and many tubers.

Xerophytes.—Xerophytes are plants that live where the water supply is limited (i.e., especially in the subtropics or as halophytes or epiphytes), and with various arrangements reducing transpiration (Willis, 1931). Xerophytes may be divided roughly into two classes—water-storing (with

special water-storing facilities) and drought resistant (without special water-storage facilities). The first class includes *Mesembryanthemum* and *Sedum*, the second class includes *Fouquieria* and *Puya*, while some plants, like the *Agaves*, come under both categories. Xerophytes, like hydrophytes, may consist of entire families, e.g., Cactaceae, Zygophyllaceae or entire genera, e.g., *Mesembryanthemum*, *Sedum* or species, e.g., *Jatropha podagrica*. Some families which are typically xerophytic, e.g., Crassulaceae, may include some aquatic forms, in this case those of the genus *Tillaea*. Xerophytes may also be halophytic, e.g., *Tamarix*, but this is not necessarily the case.

Halophytes.—Halophytes are plants (of sea-coasts, salt steppes, etc.) which obtain their food from a surrounding containing a higher percentage of salts than normal glycophytes are able to endure. By salt NaCl is usually understood, but logically consideration should also be given those plants which are strongly influenced by other salts as well, e.g., $MgSO_4$, $NaSO_4$, KCl (Uphof, 1941). No family is made up entirely of halophytes although some are mostly of this class, e.g., Chenopodiaceae and Frankeniaceae. Some genera are entirely halophytic, e.g., *Frankenia*. Typical halophytic species are *Salsola Kali*, *S. Soda*, *Polygonum maritimum*, *Frankenia intermedia* and *Plantago arenaria*. Many halophytes can thrive on land poor in salts. For instance, the *Tamarix*, inhabitants of warm arid regions, are adapted to dry-land conditions but also grow well in saline and alkaline soil. In fact, they are excellent for seaside planting and thrive in the very spray of the salt water. A similar condition is found in some of the *Mesembryanthemum*, *Casuarina*, etc. Halophytes are often xerophytes although this is not necessarily the case, e.g., *Beta vulgaris*. It is true, too, that xerophytes are not necessarily halophytes. Some halophytes are also hydrophytes, e.g., *Enalus*, *Halophida*.

ELECTROLYTE CONCENTRATION IN PLANT SAP

In hydrophytes.—Determinations were made by Harris and co-workers (1924, 1934) on hydrophytic angiosperms in California; Florida; Hawaii; Long Island, New York; and Utah (Table 1). Of the Alismaceae, seven determinations of the specific electrical conductivity (K) of the expressed sap from three species of *Sagittaria* were made. In Utah *S. cuneata* Sheld. five determinations gave an average K of .0226 reciprocal ohms. A single determination of *S. lancifolia* L. in Florida gave .0182, and a determination of *S. latifolia* Willd. in Long Island was .0182. The average for the seven determinations is .0217.

An individual determination of *Hippuris vulgaris* (Hippuridaceae) in Utah was .0174.

The waterlily *Nymphaea* (*Nuphar*) *advena* Ait. (*Nymphaeaceae*) gave .0118 in a Florida specimen.

TABLE 1. *Specific electrical conductivity and sulphate concentration in expressed sap of hydrophytes and halophytes.*

(Data from Harris and co-workers.) (Average values.)

Plant habit Family Genus	Specific electrical conductivity (K) (reciprocal ohms)	SO ₄ (grams per liter)	No. of deter- minations
Hydrophytes			
Alismaceae			
<i>Sagittaria</i>0217	4.13	7, 2
Hippuridaceae			
<i>Hippuris</i>0174	—	1,
Nymphaeaceae			
<i>Nymphaea</i>0118	—	1,
Pontederiaceae			
<i>Pontederia</i>0150	—	3,
Sparganiaceae			
<i>Sparganium</i>0247	4.48	3, 1
Average0181	4.30	—
Halophytes			
Aizoaceae			
<i>Mesembryanthemum</i>0432	—	1,
<i>Sesuvium</i>0522	5.38	12, 4
Batidaceae			
<i>Batis</i>0793	6.32	5, 4
Casuarinaceae			
<i>Casuarina</i>0380	—	3,
Chenopodiaceae			
<i>Allenrolfea</i>0802	10.83	60, 5
<i>Atriplex</i>0737	14.44	146, 16
<i>Chenopodium</i>0418	1.33	15, 3
<i>Eurotia</i>0270	—	1,
<i>Grayia</i>0632	—	20,
<i>Kochia</i>0568	3.40	30, 1
<i>Salicornia</i>0757	24.16	48, 8
<i>Salsola</i>0349	1.92	18, 4
<i>Sarcobatus</i>0556	6.09	163, 18
<i>Suaeda</i>0695	12.46	66, 11
Tamaricaceae			
<i>Tamarix</i>0379	—	2,
Average0552	8.63	—

Three determinations were made on Florida specimens of *Pontederia cordata* L. (Pontederiaceae) which gave an average value of .0150.

An average value of .0247 was obtained from three Utah samples of *Sparganium eurycarpum* Engelm. (Sparganiaceae).

In halophytes.—The specific electrical conductivities (K) of the expressed saps of halophytic angiosperms were obtained by Harris and co-workers (1924, 1934) from plants in Arizona, California, Florida, Hawaii, Long Island, Utah and Washington.

Of the Aizoaceae a California specimen of *Mesembryanthemum aequilaterale* Haw. had a K of .0432. Six determinations of *Sesuvium sessile* Pers. in Utah gave an average of .0519. Four determinations of *S. Portulacastrum* L. in Hawaii averaged .0576, while two determinations of the same plant in Florida averaged .0424. The average for all twelve is .0522.

Another halophyte *Batis maritima* L. gave an average K of .0793 for five Hawaiian specimens.

Casuarina equisetifolia L. was secured in Arizona, Florida and Hawaii. One determination was made in each locality which gave the following results: Arizona .0508, Florida .0289 and Hawaii .0345. The average of the three is .0380.

The expressed sap of a number of halophytic species of Chenopods was subjected to electrical conductivity measurements. The extremely salt tolerant *Allenrolfea occidentalis* (S. Wats.) Kuntze of which fifty-eight specimens were obtained from the southern shore of the Great Salt Lake, Utah, gave an average K of .0805. Two other determinations were made on Arizona plants with an average K of .0734.

A total of 146 determinations were made on *Atriplex* species in Arizona, California, Long Island, Utah and Washington. In Arizona four different species from which a total of nine determinations were made averaged .0599. A California sample from *A. decumbens* S. Wats. gave a K of .0971. *A. hastata* L. in Long Island in one determination gave .0470. In Utah twelve different species of *Atriplex* from which a total of 129 determinations were made, averaged .0758. In Washington *A. hastata* L. and *A. rosea* L. were examined. A total of six determinations from them averaged .0518.

A *Chenopodium album* L. determination in California gave .0330, while two samples from the same species in Long Island averaged .0509. In Utah six different species of *Chenopodium* were examined from which a total of twelve determinations averaged .0453.

The expressed sap of *Eurotia lanata* (Pursh) Moq. in one Utah determination gave .0270.

Twenty samples from *Grayia spinosa* (Hook) Moq. grown in Utah, averaged .0632.

In Utah a total of thirty determinations were made with *Kochia californica* S. Wats. and *K. vestita* (S. Wats.) Rydb. They averaged .0568.

Samples from *Salicornia* species were obtained in California, Long Island, Utah and Washington. *S. ambigua* Michx. and *S. subterminalis* Parish in a total of five California determinations averaged .0800. *S. ambigua* Michx. and *S. europaea* L. from which a total of seven determinations were made in Long Island averaged .0575. *S. rubra* A. Nels. and *S. utahensis* Tidestrom from which a total of twenty-five determinations were made in Utah averaged .0790. Eleven determinations from *A. rubra* A. Nels. in Washington averaged .0779.

Salsola Kali var. *tenuifolia* G. F. W. Meyer, was sampled in Long Island and Utah. The four Long Island specimens averaged .0297, and the fourteen Utah specimens averaged .0363. The average K for the eighteen specimens is .0349.

Sarcobatus vermiculatus (Hook.) Torr. was subjected to determinations in Arizona and Utah. The average K for three determinations from Arizona plants was .0525, and that from 160 Utah specimens was .0557. For the total the average is .0556.

Suaeda species were used for determinations in Arizona, California, Long Island, Utah and Washington. Three species in Arizona on which a total of ten determinations were made averaged .0749. In California *S. (Dondia) fruticosa* Forsk. gave an average in seven determinations of .0751. The same species in Long Island gave an average of .0432 in two determinations. A total of forty-six determinations on six different species gave an average of .0687. One determination on *S. Torreyana* S. Wats. in Washington gave .0612. The average K for all sixty-six determinations is .0695.

Tamarix articulata Vahl. in Arizona gave an average K from two determinations of .0379.

COMPARISON OF THE ELECTRICAL CONDUCTIVITIES OF HYDROPHYTES AND HALOPHYTES

The specific electrical conductivities of the expressed sap from the leaves of hydrophytes and halophytes are summarized in Table 1. In this table the average conductivity for hydrophytes is .0181 while that of the halophytes is .0552. The halophyte conductivity is thus three times that of the hydrophytes. Of the halophytes *Casuarina* and *Tamarix* are trees and to this fact they may owe their comparatively low conductivities, for it has been shown previously that in general trees have lower conductivities than herbs (McNair, 1941). There is also some evidence to indicate that each plant genus may possess an individual affinity for electrolytes (McNair, 1941).

SULPHATE CONCENTRATION IN HYDROPHYTES AND HALOPHYTES

Determinations of sulphate have been made (Harris, 1934) in the expressed saps of *Sagittaria*, *Sparganium*, *Sesuvium*, *Batis*, *Allenrolfea*, *Atriplex*, *Chenopodium*, *Kochia*, *Salicornia*, *Salsola*, *Sarcobatus*, and *Suaeda* (Table 1). We may, therefore, compare the concentration of sulphate among hydrophytes and halophytes. In making this comparison we find the amounts (grams per liter) to be of approximately one-half the magnitude in hydrophytes (aver. 4.48) as in halophytes (aver. 8.63).

THE LAW OF MASS ACTION

The concentration of sulphates in hydrophytes is decidedly lower than

in halophytes. This condition might lead one to expect a smaller amount of organic sulphur compounds to be manufactured in hydrophytes than in halophytes. Likewise, the concentration of electrolytes decreases from hydrophytes (aver. $K = .0181$) to halophytes (aver. $K = .0552$). This would lead one to expect the smallest concentration of organic plant substances elaborated from electrolytes to be found in hydrophytes. This expectation would be in accordance with the law of mass action (Berthollet, 1803). Such a conclusion would also be in harmony with the results in herbs and trees recently summarized by McNair (1941), where the amounts of alkaloids, cyanogenetic glucosides and volatile organic sulphur compounds were found to be markedly greater in herbs than in trees. The amounts of these substances were increased by the addition of nitrogenous or sulphur fertilizers to the soil. It may be profitable, therefore, to investigate the occurrence of alkaloids, cyanogenetic glucosides and volatile organic sulphur compounds in hydrophytes and halophytes. It must be borne in mind, however, that other factors such as genetic strain, time of year, etc., influence the occurrence of these substances.

OCCURRENCE OF HYDROPHYTES

Some 22 families containing 204 genera consist entirely of hydrophytes according to Engler and Gilg (1919) and Willis (1931). These families are: Alismaceae, Aponogetonaceae, Butomaceae, Callitrichaceae, Cephalotaceae, Ceratophyllaceae, Cyperaceae, Hippuridaceae, Hydrocharitaceae, Lemnaceae, Lentibulariaceae, Mayacaceae, Najadaceae, Nepenthaceae, Nymphaeaceae, Podostemonaceae, Pontederiaceae, Potamogetonaceae, Scheuchzeriaceae, Sparganiaceae, Typhaceae and Xyridaceae.

In addition to these 22 families of 204 genera which consist entirely of hydrophytes there are 50 families which contain 134 genera or species of water plants. The families thus represented may contain many different types of vegetational habit and even the genera cited may not be exclusively made up of hydrophytes. The families and genera are (Arber, 1920, Fassett, 1940, and Johnson, 1931): Acanthaceae, *Dianthera americana*; Araceae, *Acorus*, *Calla*, *Orontium*, *Peltandra*, *Pistia*; Asclepiadaceae, *Asclepias*; Betulaceae, *Alnus*; Boraginaceae, *Myosotis*; Campanulaceae, *Campanula*, *Lobelia*; Centrolepidaceae; Compositae, *Aster*, *Bidens*, *Boltonia*, *Cotula*, *Erigeron*, *Eupatorium*, *Helenium*, *Megalodonta*, *Pectis*, *Solidago*; Cornaceae, *Cornus*, *Nyssa*; Crassulaceae, *Penthorum*, *Tillaea*; Cruciferae, *Nasturtium*, *Neobeckia*, *Sisymbrium*, *Subularia*, *Rorippa*; Cynomoriaceae, *Cynomorium*; Droseraceae, *Aldrovanda*; Elatinaceae, *Bergia*, *Elatine*; Ericaceae, *Chamaedaphne*, *Ledum groenlandicum*, *Vaccinium oxycoccus*; Eriocaulaceae, *Eriocaulon*; Gentianaceae, *Limnanthemum*, *Menyanthes*, *Nymphoides*; Gramineae, *Agrostis*, *Alopecurus*, *Beckmannia*, *Calamagrostis*, *Catabrosia*, *Coleanthus*, *Echinochloa*, *Elymus*, *Eragrostis*,

Fluminea, *Glyceria*, *Leersia*, *Phalaris*, *Phragmites*, *Poa*, *Spartina*, *Zizania*, *Zizaniopsis*; Guttiferae, *Hypericum*; Haloragidaceae, *Gunnera*, *Myriophyllum*, *Proserpinaca*; Hypericaceae, *Hypericum*; Iridaceae, *Iris*; Juncaceae, *Juncus*; Labiataceae, *Lycopus*, *Mentha*, *Physostegia*, *Scutellaria*, *Stachys*; Leguminosae, *Aeschynomene*, *Desmanthus*, *Herminiera*, *Mimosa*, *Neptuna*, *Sesbania*; Lythraceae, *Ammannia*, *Decodon*, *Didiplis*, *Lythrum*, *Nesaea*, *Peplis*, *Rotala*; Malvaceae, *Hibiscus*; Melastomaceae, *Rhexia*; Myricaceae, *Myrica*; Oenotheraceae, *Epilobium*; Oleaceae, *Fraxinus*, *Forestiera*; Onagraceae, *Epilobium*, *Isnardia*, *Jussiaea*, *Lopezia*, *Ludwigia*, *Trapa*; Orchidaceae, *Cypripedium*, *Habenaria*; Pedaliaceae, *Trapella*; Philydraceae; Plantaginaceae, *Littorella*; Polygonaceae, *Polygonum*, *Rumex*; Portulacaceae, *Montia*; Primulaceae, *Hottonia*, *Lysimachia*, *Samolus*; Ranunculaceae, *Caltha*, *Myosurus*, *Ranunculus*; Rosaceae, *Comarum*, *Rubus*; Rubiaceae, *Cephalanthus*, *Galium*; Salicaceae, *Salix*; Saururaceae, *Saururus*; Scrophulariaceae, *Bacopa*, *Chelone*, *Gratiola*, *Leucospora*, *Limnophila*, *Limosella*, *Lindernia*, *Mimulus*, *Veronica*; Solanaceae, *Solanum*; Umbelliferae, *Angelica*, *Berula*, *Cicuta*, *Hydrocotyle*, *Oenanthe*, *Sium*; Urticaceae, *Planera*; Verbenaceae, *Lippia*; Violaceae, *Viola*.

OCCURRENCE OF XEROPHYTES

Some nine angiosperm families of 113 genera consist entirely of xerophytes. These are: Aizoaceae, Cactaceae, Casuarinaceae, Geissolomataceae, Myrothamnaceae, Penaeaceae, Restionaceae, Tamaricaceae and Velloziaceae. Besides these families there are, according to Engler and Gilg (1919) and Willis (1931), the following fifty families which contain 97 genera or species of xerophytes. However, the families represented may contain many different types of vegetational habit. The genera cited, likewise, may not be made up exclusively of xerophytes. The families and genera are: Acanthaceae, *Acanthus*; Amaryllidaceae, *Agave*, *Beschorneria*, *Furcraea*; Apocynaceae, *Adenium*, *Nerium*; Asclepiadaceae, *Boucerosia*, *Ceropegia*, *Cynanchum*, *Dischidia*, *Echidnopsis*, *Hoya*, *Huernia*, *Periploca*, *Sarcostemma*, *Stapelia*; Bignoniaceae; Bombacaceae; Bromeliaceae; Caparidaceae; Koeberlinia; Caryophyllaceae, *Acanthophyllum*; Chenopodiaceae, *Salicornia*; Cochlospermaceae, *Cochlospermum*; Compositae, *Artemisia*, *Baccharis*, *Espeletia*, *Gnaphalium*, *Helichrysum*, *Helipternia*, *Leontopodium*, *Othonna*, *Raoulia*, *Senecio*; Convolvulaceae; Crassulaceae, *Crassula*, *Sedum*, *Sempervivum*; Cruciferae, *Draba*; Cucurbitaceae, *Acanthosicyos*; Dilleniaceae, *Hibbertia*; Dioscoreaceae, *Testudinaria*; Empetraceae, *Empetrum*; Epacridaceae; Ericaceae, *Cassiope*, *Culluna*, *Vaccinium*; Euphorbiaceae, *Euphorbia*, *Jatropha*, *Phyllanthus*; Geraniaceae, *Sarcocaulon*; Gesneraceae, *Aeschynanthus*; Gramineae, *Ammophila*, *Stipa*. Iridaceae, *Iris*; Juncaceae, *Juncus*; Labiatae, *Rosmarinus*, *Stachys*; Leguminosae, *Acacia*, *Alhagi*, *Argyrolobium*, *Aspalathus*, *Astragalus*,

Bossiaea, *Carmichaelia*, *Cytisus*, *Genista*, *Prosopis*, *Spartium*, *Ulex*; Liliaceae, *Aloe*, *Apicra*, *Calibanus*, *Dasyllirion*, *Gasteria*, *Haworthia*, *Narthecium*, *Nolina*, *Phormium*, *Ruscus*, *Sansevieria*, *Semele*; Myrtaceae, *Eucalyptus*; Oxalidaceae, *Oxalis*; Pedaliaceae; Piperaceae, *Peperomia*; Plumbaginaceae, *Acantholimon*; Polygonaceae, *Muehlenbeckia*, *Polygonum*; Portulacaceae, *Anacampseros*, *Lewisia*; Primulaceae, *Androsace*; Proteaceae, *Banksia*, *Grevillea*; *Hakea*; Resedaceae; Rhamnaceae, *Colletia*, *Phyllica*; Rosaceae, *Adenostoma*, *Rubus*; Rutaceae, *Diosma*; Saxifragaceae; Scrophulariaceae, *Russelia*, *Veronica*; Stackhousiaceae; Stylidiaceae; Umbelliferae, *Azorella*; Verbenaceae; Zygophyllaceae, *Larrea*.

OCCURRENCE OF HALOPHYTES

Although there are a number of hydrophyte families made up entirely of hydrophytes, and a few xerophyte families that consist wholly of xerophytes, there is no family of halophytes formed exclusively of halophytes. According to Uphof (1941) there are 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes. These are: Acanthaceae, *Acanthus*; Aizoaceae, *Aizoon*, *Mesembryanthemum*, *Sesuvium*, *Tetragonia*; Amaranthaceae, *Achrysanthes*, *Amaranthus*, *Gomphrenia*, *Iresine*, *Nototrichum*, *Philoxerus*; Amaryllidaceae, *Crinum*, *Pancratium*; Apocynaceae, *Vallesia*; Batidaceae, *Batis*; Boraginaceae, *Coldenia*, *Heliotropium*, *Mertensia*, *Myosotis*, *Tournefortia*; Calyceraceae, *Acicarpha*; Campanulaceae, *Lobelia*; Caryophyllaceae, *Cerastium*, *Colobanthus*, *Lychnis*, *Sagina*, *Schiedea*, *Silene*, *Spergularia*, *Stellaria*; Casuarinaceae, *Casuarina*; Chenopodiaceae, *Allenrolfea*, *Anabasis*, *Atriplex*, *Bassia*, *Beta*, *Camphorosma*, *Chenopodium*, *Dondia*, *Eurotia*, *Grayia*, *Kochia*, *Halimus*, *Obione*, *Panderia*, *Petrosimonia*, *Sarcobatus*, *Salicornia*, *Salsola*, *Suaeda*; Combretaceae, *Conocarpus*, *Laguncularia*, *Lumnitzera*; Compositae, *Aplopappus*, *Artemisia*, *Aster*, *Baccharis*, *Bellis*, *Borrichia*, *Chrysanthemum*, *Chrysothamnus*, *Cotula*, *Eriocoma*, *Franseria*, *Inula*, *Iva*, *Jaumea*, *Lasthenia*, *Lipochaeta*, *Pluchea*, *Senecio*, *Solidago*, *Sonchus*, *Taraxacum*, *Tessaria*; Convolvulaceae, *Calystegia*, *Convolvulus*, *Cressa*, *Ipomaea*; Crassulaceae, *Rhodiola*; Cruciferae, *Alyssum*, *Cakile*, *Cochlearia*, *Crambe*, *Hutchinsia*, *Lepidium*, *Malcolmia*, *Matthiola*; Cyperaceae, *Carex*, *Heleocharis*, *Mariscus*, *Remirea*, *Scirpus*; Dipsacaceae, *Scabiosa*; Euphorbiaceae, *Euphorbia*; Frankeniaceae, *Frankenia*; Gentianaceae, *Erythraea*; Goodeniaceae, *Scaevola*, *Selliera*; Gramineae, *Aeluropus*, *Agropyrum*, *Agrostis*, *Aira*, *Atropis*, *Bromus*, *Cynodon*, *Dactylis*, *Deschampsia*, *Deyeuxia*, *Distichlis*, *Dupontia*, *Eragrostis*, *Festuca*, *Glyceria*, *Hordeum*, *Ischaemum*, *Koeleria*, *Lagurus*, *Lasiagrostis*, *Lepturus*, *Monanthochloë*, *Panicum*, *Phragmites*, *Poa*, *Puccinellia*, *Sitanion*, *Spartina*, *Spinifex*, *Sporobolus*, *Stenotaphrum*, *Zoysia*; Hydrocharitaceae, *Enalus*, *Halophila*, *Thalassia*; Iridaceae, *Iris*; Juncaceae, *Juncus*, *Marsippospermum*, *Oxychloe*; Labiatae, *Phyllostegia*;

Leguminosae, *Aeschynomene*, *Alhagi*, *Anthyllis*, *Astragalus*, *Canavalia*, *Crotalaria*, *Dorycnium*, *Lathyrus*, *Lotus*, *Medicago*, *Melilotus*, *Swartzia*, *Tetragonolobus*, *Trifolium*, *Vigna*; Liliaceae, *Allium*, *Phormium*; Linaceae, *Linum*, Malvaceae, *Althaea*, *Cristaria*, *Hibiscus*, *Malva*, *Plagianthus*; Melastomaceae, *Amphiloma*, Meliaceae, *Xylocarpus*; Myrsinaceae, *Aegiceras*; Nyctaginaceae, *Abronia*, *Boerhaavia*, *Cryptocarpus*; Onagraceae, *Sphaerostigma*; Orchidaceae, *Orchis*; Palmae, *Barringtonia*, *Bractis*, *Cocos*, *Nipa*, *Phoenix*; Pandanaceae, *Pandanus*; Papaveraceae, *Glaucium*; Plantaginaceae, *Plantago*; Plumbaginaceae, *Armeria*, *Statice*; Polygonaceae, *Coccolobus*, *Eriogonum*, *Muehlenbeckia*, *Polygonum*, *Rumex*, Portulacaceae, *Montia*; Potamogetonaceae, *Althenia*, *Cymodocea*, *Diplanthera*, *Phyllospadix*, *Posidonia*, *Potamogeton*, *Ruppia*, *Zannichellia*, *Zostera*; Primulaceae, *Androsace*, *Glaux*, *Samolus*; Ranunculaceae, *Halerpestes*, *Ranunculus*; Restionaceae, *Leptocarpus*; Rhamnaceae, *Discaria*; Rhizophoraceae, *Bruguiera*, *Ceriops*, *Rhizophora*; Rosaceae, *Potentilla*; Rubiaceae, *Asperula*, *Galium*, *Scyphiphora*; Santalaceae, *Santalum*; Scheuchzeriaceae, *Triglochin*; Scrophulariaceae, *Euphrasia*, *Gerardia*, *Herpestis*, *Mimulus*; Simarubaceae, *Suriana*; Solanaceae, *Atropa*, *Cacabus*, *Lycium*; Sonneratiaceae, *Sonneratia*; Taccaceae, *Tacca*; Tamaricaceae, *Tamariscus*; Thymeliaceae, *Pimelea*, *Wikstroemia*; Tiliaceae, *Triumfetta*; Typhaceae, *Typha*; Umbelliferae, *Apium*, *Bupleurum*, *Crithmum*, *Eryngium*, *Helosciadium*, *Heracleum*, *Orlaya*, *Pastinaca*; Verbenaceae, *Avicennia*; and Zygophyllaceae, *Nitraria*, *Zygophyllum*.

OCCURRENCE OF VOLATILE ORGANIC SULPHUR COMPOUNDS

Organic compounds containing sulphur have been found in the essential oils of six plant families (Parry, 1922; Finnemore, 1926), namely, the Liliaceae, Cruciferae, Resedaceae, Geraniaceae, Tropaeolaceae, and Labiatae. Volatile sulphur compounds have been found also in the Leguminosae, Gramineae, and Chenopodiaceae (Peterson, 1914). None of these nine families consists exclusively of hydrophytes. However, the Cruciferae, Gramineae, Labiatae, and Leguminosae contain hydrophytic genera or species, in these cases *Nasturtium*, *Mentha* and *Poa*. Of these *Nasturtium officinale* (water-cress) is the only hydrophytic species that produces a volatile organic sulphur compound. That is, out of seventy-two families that contain at least some hydrophytes four families (5.5%) contain volatile organic sulphur compounds, and out of 338 genera that contain at least one hydrophytic species only three genera (0.8%) contain volatile organic sulphur compounds.

All of the families that are known to produce volatile organic sulphur compounds, with the exception of the Tropaeolaceae, contain xerophytic genera or species. However, none of these xerophytic genera or species produce volatile organic sulphur compounds.

Out of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes five families (7.3%) and seven genera (2.9%) are known to form volatile organic sulphur compounds. The families and genera are: Chenopodiaceae, *Beta*; Cruciferae, *Cochlearia*, *Lepidium*; Gramineae, *Poa*; Labiatae; Leguminosae, *Medicago*, *Trifolium*; Liliaceae, *Allium*. As to the species of the above genera that form volatile organic sulphur compounds Uphof (1941) mentions *Beta maritima* L. (= *B. vulgaris* L.) which is the ancestor of the sugar beet. The sugar beet through cultural practice is known to be a halophyte. *Cochlearia officinalis* (scurvy grass) and *C. danica*, both known to produce the compounds under discussion, are halophytes. *Medicago maritima* is classed by Uphof as a halophyte but we also know from cultural practice that alfalfa (*M. sativa*) which forms volatile sulphur compounds is likewise a halophyte. Thus, it is evident that volatile organic sulphur compounds are much more common among halophytes than hydrophytes.

OCCURRENCE OF ALKALOIDS

In the list of 22 angiosperm families containing 204 genera which consist entirely of hydrophytes, there is only one family (4.5%), the Nymphaeaceae (water lilies), in which the genera *Nelumbium*, *Nuphar* and *Nymphaea* are known to form alkaloids.

These plants are not floating unattached in the water but have stout creeping rhizomes that are gross feeders which prefer rich alluvial soil. If we consider the 50 families and 134 genera of angiosperms which may not consist entirely of hydrophytes, then the following are known to contain alkaloids: Acanthaceae; Araceae; Asclepiadaceae; Boraginaceae; Campanulaceae, *Lobelia*; Compositae; Crassulaceae; Cruciferae; Gramineae; Labiatae, *Stachys*; Leguminosae; Malvaceae; Orchidaceae; Pedaliaceae; Polygonaceae, *Polygonum*; Ranunculaceae; Rosaceae; Rubiaceae; Scrophulariaceae; Solanaceae, *Solanum*; Umbelliferae, *Angelica*. Of these 72 families 26 (or 36%) contain alkaloids, but of the 338 genera only 8 (2.3%) are known to produce alkaloids, while in only one species *Polygonum amphibium* has an alkaloid been discovered. This species is amphibian and produces over ten times as much alkaloid when growing on land (Sanna, 1933).

Besides the nine angiosperm families and their 79 genera which are entirely xerophytic, there are fifty families and 97 genera which are more or less xerophytic. Of this total of 59 families and 176 genera there are 2 families (49%) and 17 genera (9.6%) that form alkaloids. The alkaloid families and genera are: Acanthaceae; Aizoaceae, *Mesembryanthemum*; Amaryllidaceae; Apocynaceae, *Nerium*; Asclepiadaceae; Cactaceae, *Anhalonium*, *Carnegia*, *Cereus*, *Echinocactus*, *Gymnocalycium*, *Lophophora*, *Pachycereus*, *Trichocereus*; Chenopodiaceae; Compositae, *Artemisia*, *Senecio*; Convolvulaceae; Crassulaceae, *Sedum*; Cruciferae; Cucurbitaceae;

Dioscoreaceae; Euphorbiaceae, *Jatropha*; Gesneriaceae; Gramineae; Labiatae, *Stachys*; Leguminosae, *Cystisus*, *Genista*, *Ulex*; Liliaceae; Myrtaceae; Pedaliaceae; Piperaceae; Polygonaceae; Rhamnaceae; Rosaceae; Rutaceae; Scrophulariaceae; Umbelliferae; Zygophyllaceae. Of the above, all of the species of the eight genera of the Cactaceae, all of the species of *Sedum*, and the species *Ulex europaeus* are xerophytic. There are, therefore, counting one species to a genus, ten species which contain alkaloids.

Of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes, 30 families (44%) and 19 genera (8%) are known to form alkaloids. These families and genera are: Acanthaceae; Aizoaceae, *Mesembryanthemum*; Amaryllidaceae, *Crinum*; Apocynaceae, *Vallesia*; Boraginaceae, *Heliotropium*; Calyceraceae; Campanulaceae, *Lobelia*; Chenopodiaceae, *Petrosimonia*, *Salsola*; Compositae, *Aplopappus*, *Artemisia*, *Senecio*; Convolvulaceae, *Convolvulus*; Crassulaceae, *Rhodiola* (= *Sedum*); Cruciferae; Euphorbiaceae; Gramineae, *Hordeum*; Labiatae; Leguminosae, *Crotalaria*, *Lotus*; Meliaceae; Nyctaginaceae, *Boerhaavia*; Orchidaceae; Palmae; Papaveraceae, *Glaucium*; Polygonaceae, *Polygonum*; Ranunculaceae; Rhamnaceae; Rosaceae; Scrophulariaceae; Simarubaceae; Solanaceae, *Atropa*; Umbelliferae; Zygophyllaceae. The following species of the above genera have given positive tests for alkaloids: *Mesembryanthemum* sp., *Crinum asiaticum*, *Vallesia glabra*, *Anabasis aphylla*, *Crotalaria* sp., *Boerhaavia diffusa*, *Glaucium luteum*. If we consider but one species to a genus, then there are seven halophytic species (2.9%) that contain alkaloids of the 237 genera that contain halophytes and also make alkaloids.

OCCURRENCE OF CYANOGENETIC GLUCOSIDES

Only one (4.5%) of the 22 angiosperm families which consist entirely of hydrophytes has given positive tests for the presence of hydrocyanic acid. This family is the Scheuchzeriaceae which is composed of perennial marsh herbs of grass-like habit. Some of the species of two of its genera Scheuchzeria and Triglochin produce HCN. If we consider the 50 families and 134 genera of angiosperms which may not consist entirely of hydrophytes then the following are known to form HCN: Araceae; Asclepiadaceae; Campanulaceae, *Campanula*; Compositae; Crassulaceae; Cruciferae; Droseraceae; Ericaceae; Gramineae, *Glyceria*, *Poa*, *Elymus*, *Catabrosa*; Haloragidaceae; Juncaceae, *Juncus*; Leguminosae; Melastomaceae; Onagraceae, *Jussiaea*; Ranunculaceae, *Ranunculus*; Rosaceae; Rubiaceae; Scrophulariaceae; Solanaceae; Urticaceae. Of the above genera six species have given evidence of HCN. These are: *Glyceria aquatica*, *Poa aquatica*, *Elymus* sp., *Catabrosa aquatica*, *Jussiaea* sp., *Ranunculus repens*. Of the total of 72 families and 338 genera, 21 families (29%) and 10 genera (2.9%) form HCN.

Of the nine angiosperm families and their 79 genera which are entirely

xerophytic there are no plants that produce HCN. Besides the above there are fifty families and 97 genera which are more or less xerophytic. Of this total of 59 families and 176 genera there are 19 families (32%) and 5 genera (3%) in which HCN has been found. They are Cappariaceae; Caryophyllaceae; Chenopodiaceae, *Atriplex*; Compositae; Convolvulaceae; Crassulaceae, *Sedum*; Cruciferae; Ericaceae; Euphorbiaceae; Gramineae; Juncaceae; Leguminosae, *Acacia*; Liliaceae; Myrtaceae, *Eucalyptus*; Proteaceae, *Macadamia*; Rosaceae; Rutaceae; Saxifragaceae; Scrophulariaceae. Positive tests for the presence of HCN have been given by the following species: *Atriplex semibaccata*, *Sedum altissimum* Poir., *Acacia* many sp., *Eucalyptus cladocalyx*, *Macadamia ternifolia*.

Out of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes, 23 families (33%) and 23 genera (9%) are known to form cyanogenetic glucosides. They are as follows:

TABLE 2. Proportional occurrence of volatile organic sulphur compounds, cyanogenetic glucosides and alkaloids in angiosperm families which consist essentially of hydrophytes, xerophytes and halophytes.

	Volatile Organic Sulphur Compounds		Cyanogenetic Glucosides		Alkaloids	
	Families	Genera	Families	Genera	Families	Genera
Hydrophytes	4/72 = 5.5%	3/338 = 0.8%	21/72 = 29.0%	10/338 = 2.9%	26/72 = 36.0%	8/338 = 2.3%
Xerophytes	8/59 = 13.5%	0/176 = 0.0%	10/59 = 32.0%	5/176 = 3.0%	20/55 = 49.0%	17/176 = 9.6%
Halophytes	5/68 = 7.3%	7/237 = 2.9%	23/68 = 33.0%	23/237 = 9.0%	30/68 = 44.0%	19/237 = 8.0%

Calyceraceae; Campanulaceae; Caryophyllaceae, Chenopodiaceae, *Atriplex*, *Chenopodium*; Compositae, *Chrysanthemum*; Convolvulaceae, *Ipomoea*; Crassulaceae, *Rhodiola* (= *Sedum*); Cruciferae, *Lepidium*; Goodeniaceae; Gramineae, *Agropyrum*, *Cynodon*, *Festuca*, *Glyceria*, *Panicum*, *Poa*, *Sporobolus*; Juncaceae, *Juncus*; Leguminosae, *Dorycnium*, *Lotus*, *Medicago*, *Tetragonolobus*, *Trifolium*; Liliaceae; Linaceae, *Linum*; Melastomaceae; Onagraceae; Papaveraceae; Ranunculaceae, *Ranunculus*; Rosaceae; Scheuchzeriaceae, *Triglochin*; Scrophulariaceae; Solanaceae, *Lycium*; Tiliaceae. Cyanogenetic glucosides have been found in the following halophytic species; *Atriplex semibaccata*, *Tetragonolobus siliquosus*, *Triglochin maritimum*.

GENERAL OCCURRENCE IN FAMILIES AND GENERA

In xerophyte and halophyte families alkaloids, HCN and volatile S-compounds are much more abundant than in hydrophyte families. In fact, only one hydrophyte family is known to form a volatile S-compound, only one family in which HCN has been found and one family from which an alkaloid has been isolated. Among the xerophytes three families have both

HCN and alkaloids, and one has HCN alkaloids and volatile S-compounds. In the halophytes one family has both HCN and volatile S-compounds, one family has both alkaloids and S-compounds, nine families have both alkaloids and HCN, and four families produce alkaloids, HCN and volatile S-compounds.

Of the genera in which halophytes occur, two produce both alkaloids and HCN (*Sedum* and *Lotus*); and three contain both volatile S-compounds and HCN (*Lepidium*, *Medicago* and *Trifolium*).

EFFECT OF HABITAT AND HABITAT CHANGE

As Arber (1920) has shown, hydrophytes may be classified biologically into two main groups; namely, 1. plants rooted in soil, and 2. plants which are not rooted in soil, but which live unattached in the water. Of these two main groups those which live unattached in the water would ordinarily be expected to contain a lower concentration of electrolytes than those which are rooted in the soil.

The majority of hydrophytes also show definite preferences and aversions in the matter of the soil underlying them and of the resulting differences in the nature of the solution in which they are immersed. For instance, Brown (1911) points out that sandy soil is preferred by *Eriocaulon*, *Eleocharis* and *Myriophyllum*, muddy soil by water lilies, and muddy soil margins by grasses and sedges. Seehaus (1860) found *Hydrilla verticillata* growing on muddy clay but not on sand.

The two classes of substrata which offer the most marked contrast, as regards the flora which they support, are the calcareous and the peaty. For example, *Stratiotes aloides* prefers calcareous (Davie, 1913) and *Scirpus lacustris* peaty (Kirschleger, 1857). When the substratum is peaty the humus acids are considered as breaking up the calcium carbonate, thus rendering the water untenable for lime loving plants, but favorable for others which are able to live in a solution poor in mineral salts, e.g., *Lobelia Dortmanna* L., *Litorella* and *Isoetes* (West 1905, 1908 and 1910).

Plants which live in solutions poor in mineral salts would not be expected to be as apt to form alkaloids as those living in solutions high in mineral salts. In fact, of the hydrophytes mentioned above, only those growing on muddy soil (water lilies) and muddy soil margins (grasses) are known to produce alkaloids. The water lily family, in contrast to most of the hydrophytes, prefers rich alluvial soil in abundance. Most of the Nymphaeaceae are gross feeders and it is well-nigh impossible to make the soil too rich for them. For their cultivation a compost consisting of two-thirds good soil and one-third thoroughly decayed cow- or stable-manure with a sprinkling of bone-meal, is recommended (Conard, 1905, Sturtevant, 1927, Tricker, 1927). It is not surprising that these plants on such a highly nitrogenous medium should form alkaloids.

Likewise, the only hydrophyte family (Scheuchzeriaceae) that produces HCN is made up of herbaceous rooted plants.

Two of the hydrophyte families are insectivorous (Cephalotaceae and Nepenthaceae) and are able to augment their supply of nitrogen and sulphur from captured prey. However, none of these plants is known to produce alkaloids, HCN, nor volatile S-compounds.

The amphibious plant (*Polygonum amphibium*) makes an interesting study in regard to the effect of habitat on alkaloid production. This plant protects itself from insect pests by secreting alkaloids during the flowering period. When allowed to grow in water, the plant develops with smooth leaves. It contains a trace of alkaloids when the flowering begins, the amount increasing to a maximum of 0.017% when the plant is in full bloom, and then disappears. The same plant, grown on land, gradually develops hairy leaves, which exude a viscous fluid. Alkaloids are present in greater quantities, from 0.04% at the beginning of flowering to 0.29% when in full bloom. If water is again allowed access to the plant, the leaves gradually become smooth again and the alkaloid content drops to the lower figures (Sanna 1933).

Another alkaloid, anabesine, when produced by *Anabasis aphylla*, has been found inversely proportional to the degree of moisture. (Kudryavtsev, 1939).

In a study of the HCN-toxicity of arrowgrass (*Triglochin maritima* and *T. palustris*) in Wyoming, Beath, Eppson, Gilbert and Bradley (1939) found that generally plants growing in water were less toxic than plants growing on dry ground. The plants are widely distributed over the state in wet alkaline soil and along the edges of bogs and sloughs. Similarly the annual succulent herb *Suckleya suckleyana*, which grows in moist bottoms and water holes and along the edges of lakes in Colorado was found to contain HCN when on soils rich in nitrates (Thorp, Deem, Harrington and Tobiska, 1937).

EFFECTS OF OTHER FACTORS

Besides the concentration of electrolytes in plant sap and the law of mass action, the formation of alkaloids, volatile organic S-compounds and cyanogenetic glucosides is controlled by other factors. Williams (1939) has proved that the presence and absence of the cyanoglucoside in white clover (*Trifolium repens*) is governed by a simple pair of genetic factors. Hydrogen cyanide-free lines of Sudan grass also have been found by Nowosad and MacVicar (1940). The yield of this poison is influenced also by climate, weather and seasonal factors (Fleming, Miller and Vawter, 1926) as well as by the age of the leaves and plants. Genetic strains have been found also to influence the amount of alkaloids formed in tobacco and in the opium poppy (McNair, 1941).

Boyd, Aamodt, Bohstedt and Truog (1938) found that soils high in

nitrate tend to favor HCN formation in Sudan grass. Pinckney (1924) noticed that the HCN content of sorghum cane increased as nitrate was added to the soil. For additional references in regard to increased HCN alkaloid and volatile S-compound production by fertilizers see McNair 1941.

SUMMARY

The object of this paper is to show that hydrophytes which generally have lower concentrations of electrolytes, especially sulphur and nitrogenous radicals, in their leaf saps than halophytes are less likely to produce alkaloids, cyanogenetic and organic sulphur compounds than are halophytes.

It should be remembered that some hydrophytes are amphibious, some are halophytes and some are tropophytes. Some xerophytes may also be halophytes but halophytes are not necessarily xerophytes.

The electrical conductivities of the expressed sap as well as the concentrations of sulphate in hydrophytes are less than that of halophytes.

Out of the 72 families that contain at least some hydrophytes four families (5.5%) contain volatile organic sulphur compounds, and out of 338 genera that contain at least one hydrophytic species only three genera (0.8%) contain volatile organic sulphur compounds. There is only one hydrophytic species (*Nasturtium officinale*) that produces a volatile organic sulphur compound.

All of the families that are known to produce volatile organic sulphur compounds, with the exception of the Tropaeolaceae, contain xerophytic genera or species. However, none of these xerophytic genera or species produce volatile organic sulphur compounds.

Out of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes five families (7.3%) and seven genera (2.9%) are known to form volatile organic sulphur compounds. At least three species produce the above compounds. Thus it is evident that volatile organic sulphur compounds are much more common among halophytes than hydrophytes.

In the list of 22 angiosperm families containing 204 genera which consist entirely of hydrophytes there is only one family (4.5%), the Nymphaeaceae, in which three genera (1.4%) are known to form alkaloids. However, these water lilies do not float unattached in the water but have stout gross-feeding creeping rhizomes.

If we consider the total of 72 families and 338 genera of angiosperms which may not consist entirely of hydrophytes, then 26 (36%) contain alkaloids, but of the 338 genera only eight (2.3%) are known to produce alkaloids, while in only one species (*Polygonum amphibium*) besides the water lilies has an alkaloid been discovered. This species is amphibious and produces more than ten times as much alkaloid when growing on land.

Besides the nine angiosperm families and their 79 genera which are entirely xerophytic, there are fifty families and 97 genera which are more or less xerophytic. Of this total there are 29 families (49%) and 17 genera (9.6%) that form alkaloids. If one considers one species to a genus which produces alkaloids, there are ten species which contain alkaloids.

Of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes, thirty families (44.%) and 19 genera (8%) are known to form alkaloids. If we consider but one species to a genus, then there are seven halophytic species (2.9%) that contain alkaloids.

Only one (4.5%) of the twenty-two angiosperm families which consist entirely of hydrophytes has given positive tests for the presence of hydrocyanic acid. This family is the Scheuchzeriaceae, which is composed of marsh herbs of grass-like habit.

If we consider the 72 families and 338 genera of angiosperms which may not consist entirely of hydrophytes, then twenty-one families (29%) and ten genera (2.9%) form HCN. Six species of the above have given evidence of HCN.

Of the nine angiosperm families and their 79 genera which are entirely xerophytic there are no plants that produce HCN. However, out of the total of 59 families and 176 genera that are at least partially xerophytic, nineteen families (32%) and five genera (3%) have given positive tests for HCN. Five species, if one species to a genus be considered, produce HCN.

Out of the 68 families and 237 genera of angiosperms which consist to a greater or lesser degree of halophytes 23 families (33%) and 23 genera (9.%) are known to form cyanogenetic glucosides. HCN has been found in three halophytic species.

Plants growing in water have been found to produce smaller amounts of both alkaloids and HCN than those growing on land or in moist soils rich in nitrates.

The above occurrence of alkaloids, cyanogenetic and organic sulphur compounds is in accordance with the law of mass action, although it must be remembered that other factors such as age of leaves, genetic strain, climate, weather and seasonal factors may be influential.

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A Monograph of *Lambertella*, a Genus of Brown-Spored Inoperculate Discomycetes

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The genus *Lambertella* of the Sclerotiniaceae² was proposed by von Höhnelt (1918) for a species of "Stromatinia mit gefärbten Sporen." The type species which he named *L. corni-marisi*, occurring on mummied fruits of *Cornus mas* was collected by the Rev. P. Lambert Gelbenegger³ in lower Austria in October 1917. No other species of this genus appears to have been definitely recorded as such in the literature since that time.

The only collections of *L. corni-marisi* recorded aside from the type specimen, so far as I can discover were made by T. H. Harrison in August 1931 on mummied apples and pears in Switzerland and in two places in South Germany. Cultures of the fungus were sent me by Harrison in September 1933. My studies of this species over the years since have confirmed most of the statements and conclusions of Harrison and El-Helaly (1935) in their rather extensive paper on this fungus.

Seven other species which I am referring to this genus have also come to my attention. Of these the earliest known to me was first collected in 1912 in Bermuda by F. J. Seaver on berries of *Jasminum gracile*. I found it there again in 1922. Thanks to the kind cooperation of J. M. Waterston of the Bermuda Agricultural Station I finally obtained abundant material and pure cultures of this species in the summer and autumn of 1941, not only from Jasmine berries but also from loquat fruits and from the leaves of the fiddlewood tree (*Citharexylum spinosum*). In August 1936 I received

¹ ACKNOWLEDGMENTS. I am indebted to the American Philosophical Society for a grant from its Penrose Fund for assistance in my investigations on the stromatic discomycetes, one product of which is this monograph. It is also a pleasure to acknowledge the contributions of the many persons whose generous assistance and cooperation have made the completion of this paper possible. I thank my technical assistants Dr. W. L. White, Miss Ruby Rice and Mrs. Regina S. Brinkerhoff for their help with the microscopic measurements and drawings; Mr. R. W. Fischer for making the photographs; my mycological colleagues Drs. F. J. Seaver, G. W. Martin, David H. Linder, T. H. Harrison, S. M. Zeller, F. L. Drayton, Bessie B. Kanouse and Miss Edith K. Cash for the gift or loan of valuable specimens and cultures. I am especially appreciative of the generous assistance of Mr. J. M. Waterston of the Agricultural Station of Bermuda in providing me with numerous collections and cultures of the species occurring on that island. For critical reading of the manuscript I am deeply grateful to Drs. W. L. White, David H. Linder, H. M. Fitzpatrick, F. L. Drayton and G. W. Martin.

² Nannfeldt (1932: 297-298) refers *Lambertella* along with *Rutstroemia* to the sub-family or tribe Helotioideae while the other stromatic Helotiaceae are included by him in the tribe Ciborioideae (p. 307). I propose the establishment of a new family under the name **Sclerotiniaceae** to comprise those species, now commonly included in the Helotiaceae, in which the apothecia arise from a stroma (sclerotium, semistroma, stromatized substrate, etc.). I expect to publish shortly a synopsis of the genera of the Sclerotiniaceae in which I shall more fully define and characterize this new family of the inoperculate discomycetes.

³ Harrison and El-Helaly (1935: 211) refer to the collector as "Lambert." This was his Christian name, not his surname as these authors' usage would imply.

fresh specimens of a third species from Dr. David Linder, collected by him on leaves of *Cephalanthus occidentalis* near West Roxbury, Mass. A month later I collected this same species near the outlet of Cayuta Lake, New York. From both these collections ascospore isolates were obtained. I discovered a fourth species on dead hanging leaves of *Viburnum cassinoides* in the "Bottomless Pit," near Hanover, New Hampshire in August 1937. Pure cultures of this species were also obtained. A fifth species was discovered in September 1938 by me and some of my graduate students on mummified hulls of the shagbark hickory on the east side of Cayuta Lake, New York. This also grew readily in pure culture. From dried specimens collected in March 1941 by A. W. Evans and Dr. S. M. Zeller on sweet cherry mummies near Salem, Oregon, I succeeded ten months later in getting pure cultures of a sixth species. A seventh species was originally described and doubtfully referred by Miss Edith K. Cash to *Lambertella* (Cash 1937). Late in 1941, six years after it was collected by Dr. G. W. Martin in Colombia, S. A., my attempts to germinate the ascospores of this species failed. Ascospores of the eighth species, collected by Dr. E. B. Mains in June 1936 on leaves of *Coccolobis* sp. in British Honduras and described by Dr. Bessie Kanouse (1941) under the name *Ciboria tropicalis*, also refused to germinate. Thus of the eight species here recorded I have been most fortunate in having been able to grow and study six of them in culture under laboratory conditions. All of the six including the type species have produced mature apothecia in abundance.

Judging from the literature, brown-spored species of the Sclerotiniaceae would appear to be rare. Of the published record known to me of brown-spored discomycetes the only other genus undoubtedly referable to this family is that represented by *Phaeociboria tetrica* (Quél.) von Höhnelt (Whetzel and White 1940:614). *Phaeosclerotinia nipponica* Hori (1916) referred to by Harrison and El-Helaly (1935:211) presents a problem in identity a consideration of which cannot be adequately presented here. As a result of correspondence with Dr. Hori (during 1937-1938), and a critical study of the description of his fungus as also of cultures and specimens he sent me, I am satisfied that he confused two fungi, a *Monilinia* species and a species of *Lambertella*. He apparently preserved no specimens of the apothecial stage, while the cultures and the specimens of apple mummies which he sent me are unquestionably those of a *Monilinia* species. With no type material of his apothecial form available the validity of Hori's *Phaeosclerotinia nipponica* cannot at present be definitely determined. Even though I am convinced that Hori had in his apothecial form a species congeneric with von Höhnelt's *Lambertella*, I do not feel warranted, in the circumstances, in recognizing *Phaeosclerotinia* in preference to *Lambertella* as Harrison and El-Helaly (1935:212) suggest may eventually be necessary.

As pointed out by Whetzel and White (1940:613) "The validity of colored spores as a generic character in the Helotiaceae may be questioned. It seems probable . . . that the brown-spored species may eventually be interpolated among, and considered congeneric with, certain hyaline-spored species to which on the basis of structural characters, or on other grounds they would appear to be related." However, the fact that the species here referred to *Lambertella* present distinctive characters other than their brown spores seems to warrant the acceptance of von Höhnelt's genus as entirely valid. The characters of their stromata and the structure of their apothecia alone are sufficient to indicate the close relationship and generic identity of the species here discussed.

The unfortunate record by Harrison and El-Helaly (1935:212) of my incautious and ill-considered statements regarding the generic identity of von Höhnelt's fungus with *Ciboria* Fckl. can only be retracted with the admonition to my young colleagues that even loose taxonomic talk is dangerous. Statements one is not prepared to see in print should always be made with the understanding that the remarks are "off the record" and subject to later, more mature consideration. *Lambertella* is quite distinct from *Ciboria* as I now interpret these genera.

The idea suggested by Harrison and El-Helaly in the title to their paper, that *L. corni-maris* is "parasitic" also deserves some comment. A parasite in the strict interpretation of that term as used by De Bary and even as set forth in modern dictionaries implies that a true parasite is an organism that derives its nourishment from the *living* cells of another organism called its host. Neither *L. corni-maris* nor any of the other species here treated exhibit any evidence of true parasitism. They all appear to obtain their nourishment from dead or dying cells of the plant parts which they invade. All of them grow readily on ordinary culture media or on sterilized plant tissues. That they may invade and kill the living cells of fruits or leaves of various plants and nourish themselves on the food substances thus made available is patent. They are necrogens, or if you like, pathogenic saprophytes. As true pathogenic parasites one may cite the rusts, powdery mildews, the smuts and the downy mildews. Those fungi causing necrosis or rotting of plant parts, "spotting" of leaves, cankers, etc. are usually only pathogenic saprophytes, not parasites in spite of the general misuse of that term by mycologists and phytopathologists.

That the species of *Lambertella* are also but mildly pathogenic is indicated both by observation and experiment. Most if not all of them appear to attack only the mature or ripening organs of their susceptibles. The experiments on infection by Harrison and El-Helaly (1935:209) with *L. corni-maris* inoculated into apples in comparison with the rotting activities of the European brown rot fungus, *Monilia fructigena*, show the latter to be 17 times as destructive (in terms of weight of rotted tissue) as is the former.

Experiments in my laboratory with *L. corni-maris* inoculated into fruits of *Cornus mas* indicate that only ripe fruits are readily invaded. Preliminary inoculation experiments with some of the other species indicate that they, like *L. corni-maris*, are able to infect only mature fruits or leaves. For example, repeated attempts to infect Jasmine seedlings with ascospores of the Bermuda species which rots the mature fruits, consistently failed while mature fruits of the loquat and apple are readily invaded and rotted by this species (my own and Waterston's experiments). The species from hickory nut hulls, and that from *Viburnum* leaves as well as the one from sweet cherries all cause rotting of apples similar in rate and appearance to that caused by *L. corni-maris*.

TECHNIQUES

The data here recorded are to an unusual degree derived from a study of living materials. I have personally observed in their natural habitat four of the species here described. Six have been grown in pure culture and carried through to apothecial development under laboratory conditions. All the culture work has been done on potato dextrose agar (PDA).⁴ Spore germination has been examined either on agar or in hanging drop cultures, at room temperature.

Measurements of asci, ascospores, and paraphyses have usually been made in water from fresh material. Unless otherwise specified all measurements were made under a high, dry objective. Measurements of spermatia were in every case made under an oil immersion objective.

Color records are based on Ridgeway's Color Standards.

All drawings have been made with the aid of the camera lucida.

OBSERVATIONS ON THE MORPHOLOGY OF LAMBERTELLA SPECIES

Before presenting the technical description of the genus and of the eight species known to the writer, it may be helpful to point out the chief features of the various organs of this group of discomycetes.

The STROMATA of all the species of *Lambertella* are fundamentally and strikingly alike and characteristic, another illustration of the fact that throughout the *Sclerotiniaceae* the characters of the stroma usually constitute the most reliable basis for generic segregation. In invaded fruits (including the hulls of the hickory nut) the stroma consists of a thin dark (brown to black) *rind* surrounding a layer of necrotic susceptible tissues, the *medulla*. The enclosed medulla is composed of the more or less digested susceptible cells interlaced through and through with a loose web of much-branched and anastomosed, slender, thin-walled, hyaline, septate hyphae. The rind is composed of a single layer of dark, thick-walled empty cells, presenting in surface view a most striking and characteristic pattern

⁴ Formula: potato, 400 grams; dextrose, 10 grams; agar, 15 grams; distilled water, 1000 cc.

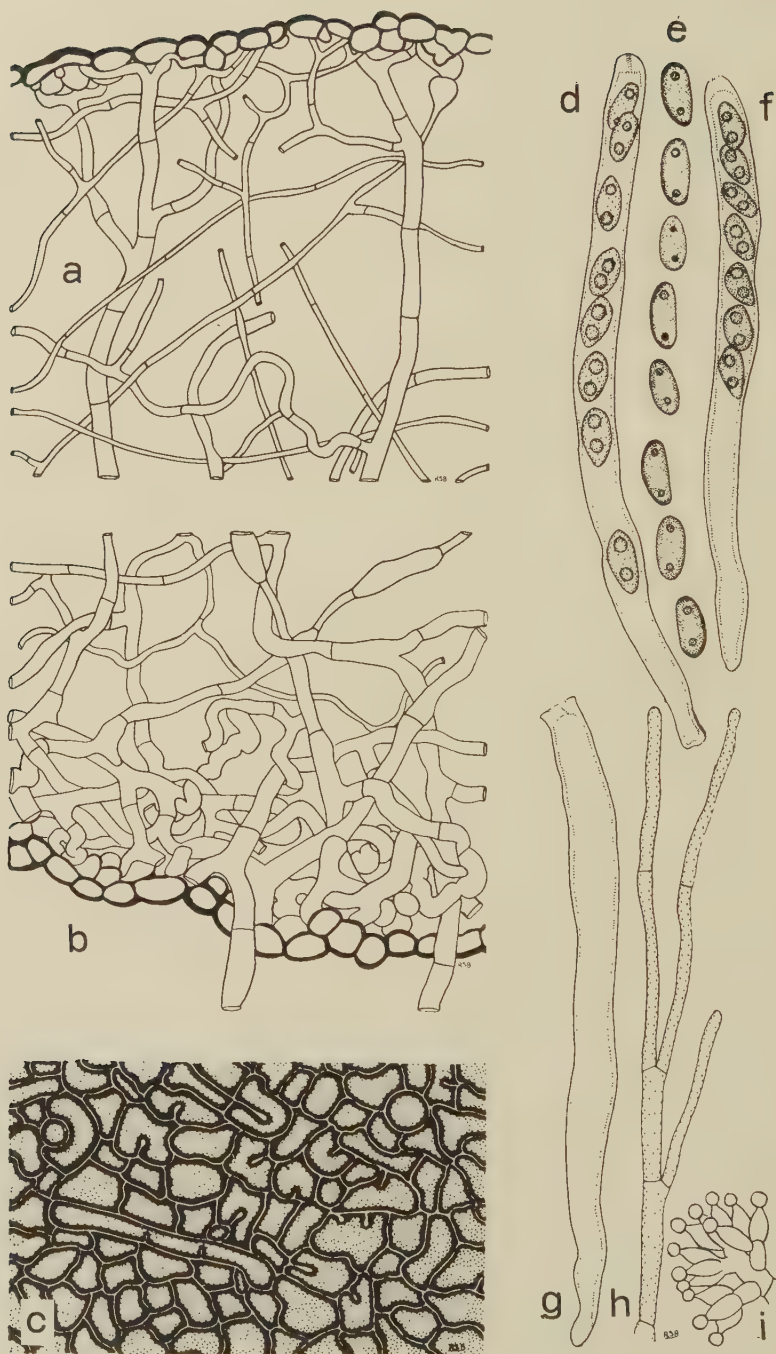


FIG. 1. (See opposite page for explanation.)

(Text Fig. 1c). This same rind pattern is also presented by the stromata when developed on potato dextrose agar. The relation of the rind cells to the medullary hyphae is shown in Text Fig. 1. a-b. The enclosed partially digested cells in the mature stroma are embedded along with the slender hyphae in what appears to be a transparent gelatinous matrix (?) in which they are preserved from decay until the food thus stored in the medulla is finally exhausted by the production of apothecia. The invaded fruits are mummified and more or less shriveled, the externally dark-colored stroma forming a thin shell surrounding the seed and non-stromatized tissues of the fleshy part of the fruit. In the hickory nut hull each entire bract of the hull may be encased by the rind or only a part thereof may thus be blocked off and mummified.

In the leaf-inhabiting species the stroma consists of a more or less sharply defined block of tissue, the stromatized area usually delimited by a black line which is a band of rind cells passing through the leaf tissues perpendicular to the surface. This rind may or may not extend partially over the surfaces of the blocked-off area. The structure of the stroma in the leaf is otherwise essentially that of the stroma in the fruits.

It may be remarked here that we have in the stroma of *Lambertella* as in *Rutstroemia* what might be designated a semistroma or a "pseudosclerotium" as conceived of by Honey (1928:142-143, 153). Honey, however, is in error in his interpretation of the stromata of *Monilinia* and *Ciboria* species. He was apparently misled by an examination of the incompletely formed or young stroma. The structure of the fully matured stroma of *M. fruticicola* is essentially that of the sclerotium of the true *Sclerotinias* (e.g. *S. sclerotiorum*).

The SPERMATIA are of the usual globose or slightly ellipsoid form characteristic of the *Sclerotiniaceae*. They are produced endogenously in succession from the tips of club-shaped spermatophores which arise singly or in fascicles from a single cell of the superficial mycelium. The spermatophores of most species form on culture media, hyaline, naked, more or less globose spermodochia (Text Fig. 1. i) which are apparently of the same type in nature. Certain of the leaf-inhabiting species form minute black lenticular spermogonia (Text Fig. 7. b) just beneath the cuticle in the striomatized areas. These are in aspect and structure like those in certain species of

FIG. 1. *Lambertella corni-marit*.—a-c, Structure of stroma (produced on PDA); a, section through upper part of stroma, showing upper or exposed rind layer and subtending hyphae; b, through lower submerged part, showing lower or submerged rind with subtending hyphae, total thickness of stroma about 1 mm., spaces between hyphae, "stromatized" agar $\times 830$; c, rind-pattern, surface view. Note translucent line between adjacent walls of the rind cells. Walls dark brown; d, young ascus, spores uncolored, guttulæ prominent $\times 850$; e, fully mature ascospores $\times 850$; f, ascus, containing mature spores $\times 800$; g, ascus immediately after spore discharge $\times 830$; h, paraphyses $\times 830$; i, spermatia (diagrammatic) $\times 820$.

Rutstroemia, e.g. *R. pruni-serotinae* (White 1941:231, fig. 70). The spermatia are hyaline, usually appearing in about seven days on water agar. They are known in most species only in pure cultures but doubtless occur regularly on the natural substrata. That they are functional seems unquestionable in spite of the fact that at least five of the species of the genus here described appear to be homothallic, single ascospore cultures in all cases tested, except one, producing fertile apothecia.

The APOTHECIA of all the species are much alike in form and internal structure. They are distinctly stipitate in most species, the length of the stipe being variable, usually dependent upon the humidity of the air and the light intensity or depth to which the stromata may be buried. In three of the species the apothecia appear to be very short stipitate to sessile. This is certainly true of the species from Oregon on sweet cherries (Pl. 4, figs. 4, 5). In the early stages of their development the apothecia of this species are distinctly short stipitate but at maturity when the disc is fully expanded there is little indication of a stipe. Apothecia of the species on nuts from Colombia are also strikingly short stipitate, likewise appearing sessile, when fully expanded (Pl. 6, fig. 4). The apothecial fundaments arise from the stroma as minute, barely visible brown or black cushions. Elongating, they become cylindrical, bulbous or cupulate as the pore makes its appearance at the tip, after which they rapidly expand into mature apothecia. Under favorable conditions of temperature, light and moisture, apothecia mature and begin spore discharge within a week or ten days after the fundaments appear. Apothecia of the species grown in culture usually continue to mature and discharge spores for a period of two weeks or so.

The stipes and underside of the cups of all species are more or less fibrillose and puberulent, or furfuraceous, hyphal tips usually forming a fringe about the margin of the cup.

The apothecia are small to minute, the diameter of the disc ranging from 1 mm. or less in the species on *Cephalanthus* to 7.5 mm. in the largest apothecia of *L. corni-maris*. The size varies greatly even within a given species, and on the same stroma. The color of the apothecia varies with the different species but in general the basic color is some shade of vinaceous or yellowish brown, especially in the young apothecia before the ascospores darken. The light-brown outer layer of cortical cells usually gives a darker tint to the stipe and underside of the receptacle of the young apothecium, while in the fully expanded apothecium this dark color is most pronounced on the basal part of the stipe. The hymenium when first exposed and before the ascospores begin to color, is usually of a pale yellowish color, while the color of the hymenium of the mature apothecium is some shade of brown usually very dark, in some species almost black. Its shade of color is determined by the number and degree of coloration of mature ascospores at

any given moment. The hymenium usually becomes much lighter in color right after a heavy discharge of spores.

The anatomy of the apothecium, based upon a study of longitudinal median sections of different species, presents the following features:—A fleshy *receptacle* or cup passing below into a rather stout stipe. This receptacle consists of an external layer or layers, the *cortex*, and an internal mass of loosely and irregularly interwoven hyaline hyphae, the *medulla*. Resting upon the upper surface of the medulla is the subhymenial layer from which arise the asci and paraphyses to form the hymenium. The cortex (by some called the excipulum) surrounds the medulla, passing upward and about the hymenium to form the margin of the disc and downwards to form the major thickness of the stipe. The inner cortical layer consists of several rows of long, closely packed, parallel hyaline hyphae. Their diameter is essentially that of the medullary hyphae. Extending from the base of the stipe upward often halfway or so over the receptacle is an outer cortical layer of long rhomboidal cells with pale brown walls which in the lower stem region sometimes forms a palisade-like layer standing at an angle to the inner cortical layer. Exserted from the cortical layers are the free ends of slender hyaline hyphae, the apical cells of which are characteristically swollen in most species. These hyphal tips give the stipe and receptacle its puberulent or furfuraceous character and form the fringe about the disc.

The ASCI of these species are much alike in form and size, being relatively large and stout for such small apothecia. They are cylindrical to clavate, usually gradually attenuate in the lower third, sometimes with a sharply constricted base or foot. The tip is rounded or truncate and distinctly thickened with the pore conspicuous and staining blue with iodine (J+). The asci are uniformly 8-spored, the spores arranged uniseriately until just before spore ejection when they may become more or less biseriately. The ripe spores usually lie in the upper half or two-thirds of the ascus but in certain species they occupy nearly its entire length.

The ASCOSPORES are ellipsoid, flattened or even concave on one face; walls thicker and darker on the convex face; they do not vary markedly in size as between species, ranging from 8 to 14μ in length by 4 to 7μ in breadth. They are some shade of golden brown or olivaceous brown when fully mature. The spores of all species are conspicuously biguttulate when young and hyaline. The guttulae in the young spores are very large, diminishing in size in the mature spores, where they are often inconspicuous or masked by the dark color of the spore wall. They may disappear in dried specimens. While the spores become fully colored before discharge in most species, in others they may remain almost or quite hyaline until after ejection. The walls of the spore appear to be smooth except in one species where they are adorned with fine punctations which seem to be the ends of cylindrical thickenings or deeper colored cylinders passing through the

wall (Text Fig. 3). Each ascospore is surrounded with a thin, hyaline gelatinous membrane. Spore germination occurs promptly at ordinary room temperature (18° – 20° C.). The germ-tube arises usually from one end of the spore, sometimes from both ends, in at least one species regularly from the side. It is of approximately the same thickness as the diameter of the spore. In certain species the first cell of the germ-tube is strikingly larger in diameter than the rest of the hypha. The spores swell considerably on germination, the wall color gradually fading. Septation of the tube occurs early, often before branching begins. The first septum commonly appears directly adjacent to the spore itself. The guttulae persist for some time but gradually disappear as elongation of the germ-tube proceeds. In most species, as observed by Harrison and El Helaly (1935:201) in *L. corni-maris*, the germinating spore at first takes on a more or less angular outline, becoming globular or broadly elliptical as germination advances.

The PARAPHYSES appear to be normally three branched in all the species, but are in some cases easily taken to be simple as they usually become broken apart when crushing the mount. The point of branching in some species is very near the base. They are hyaline, sparingly septate and more or less clavate at the tips, in certain species conspicuously so, the apical cells strikingly vacuolate.

CULTURAL CHARACTERISTICS

Although a large amount of culture work has been done on six of the species of *Lambertella*, a brief summary only of the cultural characteristics is here presented. The features described are those exhibited by their growth on potato dextrose agar at a controlled temperature of 18° C. (Pl. 1). Grown at ordinary room temperature either summer or winter they present no marked variations from growth at 18° C. Grown simultaneously in the same petri dish or separately, each species presents distinctive characteristics in mycelial growth and stromal development.

All are relatively rapid growers with little variation in the growth rate as between species, usually covering the entire surface of a petri dish in about a week at 18° C.

The optimum temperature for growth and development of the stroma appears to be around 20° C. for all the species tested.

Stromata, however, begin to form at markedly different periods of growth in the different species. The species from Bermuda, a tropical habitat, grows more rapidly than the others and begins the formation of its stroma in about five or six days. Those from temperate regions are much slower in the formation of their stromata (two to three weeks). The Bermuda species not only initiates its stroma much earlier but matures it and produces apothecia therefrom in two to three weeks from date of planting under favorable conditions. *Lambertella corni-maris*, whose habitat is in

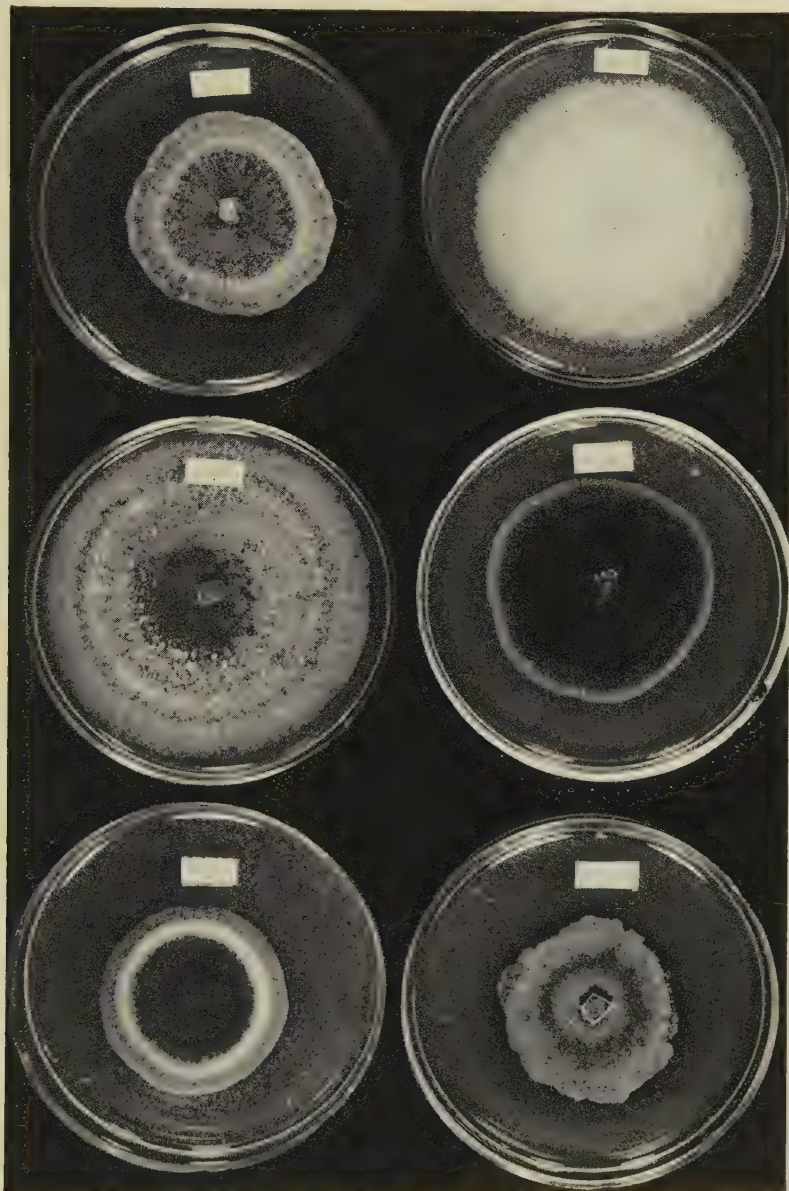


PLATE I. Appearance of six species of *Lambertella* on PDA, fifth day after planting, grown at room temperature (18–20°C.) under a bell jar. S1010 = *L. corni-maris*, S1393 = *L. hicoloriae*, S1480 = *L. jasmini*, S1445 = *L. pruni*, S1345 = *L. viburni*, S1242 = *L. cephalanthi*. Note the striking differences as between *L. corni-maris* and *L. hicoloriae*, and as between *L. viburni* and *L. cephalanthi*, pairs of species not readily distinguishable from their apothecial characters. Yellow ocher pigmentation strong in *L. pruni* and *L. cephalanthi*, medium in *L. corni-maris* and *L. viburni*, very faint in *L. hicoloriae* and *L. jasmini*.

southern Germany and Switzerland, and the species on sweet cherries from the Pacific Coast are the next to initiate their stromata. In these species the stromata appear to be mature in about 14 days, but apothecia appear only after seven or eight weeks from date of planting. In the species occurring in northeastern United States, although the stromata appear to be mature within two weeks or so, apothecia do not usually develop until after some months. It thus appears that in the case of the temperate-climate species the stroma requires a relatively long resting period before the production of apothecia. All species cultured develop their apothecia from the stroma in the original culture vessels. However, these are produced much more abundantly and promptly if with maturity of the stromata they are removed from the agar and placed on moist sand in a covered chamber. Light does not seem to be necessary for the initiation of the stromata or apothecial fundamentals but is apparently necessary for the development and maturity of the apothecia in most species.

All species exhibit some aerial mycelium during the early stages of development but it largely disappears with maturity of their stromata. This aerial mycelium is more or less characteristic for each species, being either pruinose, fibrillose, woolly or felty-floccose. In *L. corni-maris* it is typically radiate, most abundant in the species on hickory nuts, and almost completely wanting in the species from Oregon. In all cases the aerial hyphae are short, collapsing as the stroma matures. The submerged mycelium of all six species, during early growth and development, produces a yellow ochre (R) pigment of varying degrees of intensity. This is at first present only in the hyphae but soon diffuses into the medium. It gradually fades and disappears as the culture ages or crystallizes out in the uninvaded medium. The acidity of the agar is markedly increased. This acidification seems to be most pronounced in the case of *L. corni-maris*, the agar external to the mature stroma becoming very soft, almost liquified. The stroma in all these species appears at first as a pale olivaceous-brown, thin, one-celled rind layer on the surface of the agar. This rind gradually deepens in color to a dark olivaceous-brown or black. Along the edge of the more or less circular stroma the rind turns at right angles into the agar for a depth of one to several millimeters, again turning at right angles to form a submerged rind, usually though not always completely enveloping the stromatized agar layer. Sometimes this rind may go quite to the bottom of the petri dish, forming a more or less complete rind along the very bottom of the agar layer. Not infrequently there are large islands left bare of a submerged rind or even of a surface rind. Sections through the agar thus enclosed by the upper and lower rind present a loosely interwoven anastomosed network of slender rather thin-walled hyphae imbedded in the agar matrix (Text Fig. 1, a & b). One of the striking features of this enclosed agar matrix is that it becomes more perfectly solidified, being, when mature, elastic or cartilaginous in character. Even in the areas of the agar-hyphal

complex not covered by the submerged rind the agar is usually equally firm and elastic. The agar external to this stroma is, as I pointed out above, more or less softened by the acidification of the medium. Just what these fungi do to solidify and rubberize the agar enclosed by the rind is a problem still remaining to be solved. As pointed out above the stroma formed in fruits or leaves preserves in a similar manner the enclosed susceptible tissues.

TAXONOMIC RELATIONSHIPS

A consideration of the relationship of *Lambertella* to other genera of the Sclerotiniaceae leads to the conclusion that species of this genus are most closely related to those of *Rutstroemia*. This is suggested by their type of stromata and the colors, general aspect and elastic character of their apothecia. The aestival habit of fruiting of most species of both groups is another indication of this relationship. The species of *Lambertella* are, however, quite distinct from those of *Rutstroemia* in several important characters, notably in the brown color of their spores and the non-septation of these spores even at fullest maturity. The hyaline character of the spores of certain species until after ejection might cause them to be taken for *Rutstroemia* in dried herbarium specimens. Furthermore the spermatia are globose or but slightly elliptic in all species of *Lambertella* while in *Rutstroemia* they tend to be distinctly longer than broad. Spermatia appear never to be produced directly on the ascospores as is so characteristic for many species of *Rutstroemia*.

EXSICCATI SPECIMENS

Duplicate specimens of these species, unless otherwise stated, have been deposited in the following herbaria: Farlow Herb., Harvard Univ.; New York Bot. Gard.; Royal Bot. Gard. Kew, Eng.; British Museum, London; Univ. Toronto, Canada; Mycol. Coll's. Bu. Pl. Ind., Washington, D. C.; Missouri Bot. Gard., St. Louis, Mo.; Univ. Museum, Ann Arbor, Mich. I shall be pleased to send cultures of such species as are available in this form to anyone interested.

TAXONOMY OF THE GENUS LAMBERTELLA⁵

GENERIC DIAGNOSIS

Lambertella von Höhnelt. Sitz.-ber. Akad. Wien I. **127**: 375. 1918.

Stromata diffused, indeterminate, surrounding or blocking off the invaded portions of the substrate, externally brown to black; structurally consisting of a one-cell-thick, characteristic rind of dark-colored empty cells (Text Fig. 1. c) enclosing or blocking off a medulla composed of a network

⁵ Following the practice so ably defended by my eminent mycological colleague, John Dearness (1941: 366) I present no Latin descriptions for the new species here described. Likewise in the interest of simplification in nomenclatorial practices I do not capitalize species names.

of loosely interwoven anastomosed thin-walled hyphae enmeshing the more or less digested and preserved tissues of the suscept. This hyphal network and the residual tissue elements appear to be embedded in a hyaline gelatinous matrix of some sort.

Spermatia globose to slightly elliptic, hyaline, produced successively from the tips of clavate spermatophores which are borne in fasciculate naked spermodochia or in covered lenticular spermogonia.

Apothecia stipitate, arising from a stromatized substratum to which they are firmly attached, gregarious or scattered, fleshy, elastic, becoming coriaceous or corneous on drying, reviving when moistened, usually some shade of vinaceous brown or yellowish brown when fresh; *disc* cup-shaped or shallow saucer-shaped to appanate when mature; *hymenium* strikingly darker just before spore discharge, lighter in color immediately after; *stipe* relatively stout, variable in length or apparently wanting, concolorous with the receptacle, puberulent, hirsute or furfuraceous, fibrillose; *asci* usually stout cylindrical to clavate, attenuated below, rounded to truncate and thickened at the tip, pore usually prominent, J+, 8-spored; spores usually uniseriate, often becoming biseriate just before discharge; *ascospores* one-celled, broadly ellipsoid, ovoid or lunate, usually flattened or even concave on one face, strikingly biguttulate when young, wall smooth or ornamented, golden brown or olivaceous brown when fully mature, the convex wall more or less thickened; *paraphyses* two to three branched, slender, septate, hyaline, terminal cells mostly somewhat clavate.

Conidial stage lacking.

TYPE SPECIES: *Lambertella corni-maris* von Höhnelt.

NOTES: There is here presented for the first time a technical generic description. Von Höhnelt's (1918) description is of the type species, *L. corni-maris* only, while Harrison and El-Helaly (1934) deal likewise with a consideration of the species *per se*. The addition of seven species to the genus naturally calls for a broader interpretation of the generic characters than is to be inferred from von Höhnelt's original description of the type species. The outstanding characteristics of the genus appear to be the peculiar semi-stroma (Text Fig. 1. a, b, c) with its very characteristic rind pattern and the colored ascospores. The more or less thickened face of the spore wall appears also to be of generic significance. Five of the six, grown in pure culture, have proven to be homothallic.

DESCRIPTIONS OF SPECIES

LAMBERTELLA CORNI-MARIS von Höhnelt. Sitz.-ber. Akad. Wien I. 127: 375. 1918.

Plate II and Text Fig. 1

Revised description:—*Stroma* indeterminate, usually surrounding the mummified fruits, delimited by a subcuticular and an internal one-cell-

thick, dark-brown or black rind of the pattern characteristic of the genus (Text Fig. 1. a, b, c). On potato dextrose agar diffuse, thin, discoid, externally black with tints of brown and purple, aerial hyphae sparse, radiate.

Spermatia hyaline, sphaerical about 3μ in diameter, borne successively from the tips of clavate spermatophores which arise from naked fasciculate spermodochia. Known only from pure cultures. This species is homothallic.

Apothecia arising from the stroma, gregarious, fleshy, stout, stipitate, elastic, puberulent beneath, ranging from 1–7.5 mm. in diameter. Color variable, sayal brown becoming natal brown or warm sepia to chocolate or burnt umber when young; *disc*, when young, crateriform becoming shallow saucer-shaped to applanate; *hymenium* when young pale, concolorous with the rest of the cup and stipe, becoming wood brown to dark raw umber just before spore discharge, lighter (Isabel color) immediately thereafter; *stipe* variable in length, stout, above concolorous with the young receptacle, black near the base, puberulent to hirsute especially at the base. Apical cells of free hyphal tips often swollen; *asci* cylindric to clavate, attenuate toward the base in the lower half, rounded or truncate at the top, apex thickened, pore J+, $80-110 \times 7-8\mu$, av. $100 \times 7.5\mu$; 8-spored, spores uniseriate; *ascospores* ellipsoid, slightly flattened on one side, occasionally bluntly apiculate at one or both ends, wall slightly thickened on convex face, smooth, olivaceous brown, biguttulate (100 meas. Whetzel) $7.5-11.3 \times 3.7-5.0\mu$, mode $8.8 \times 5\mu$, av. $9.2 \times 4.6\mu$; (200 meas. Harrison and El-Helaly) $7.5-11.5 \times 4-6.5$, av. $9.8 \times 5\mu$; *paraphyses* slender, hyaline, usually a main axis with two side branches (Text Fig. 1. h), septate, projecting slightly above the tips of the asci, attenuate or slightly if at all swollen toward the apex, $100-140 \times 1.4-3\mu$.

HABITAT: On mummied fruits of *Cornus mas* in lower Austria, October 1917 (von Höhnelt, 1918) and on mummied fruits of pears and apples, South Germany and Switzerland, August 1931 (Harrison and El-Helaly, 1935). Fruits of *Cornus mas* at Ithaca, New York, inoculated with a culture of this fungus received from Harrison mummified the fruits and produced apothecia.

TYPE LOCALITY: St. George in the Cloister near Waidhofen on the Ybbs in lower Austria.

DISTRIBUTION: Known only from Austria, Germany and Switzerland.

TYPE SPECIMEN: Von Höhnelt's type specimen is deposited in the Farlow Herbarium at Harvard University, a few apothecia from which are also deposited in the Cornell Plant Pathology Herbarium. Abundant material of this species on its natural substrate (mummified berries of *Cornus mas* artificially inoculated) and stromata with apothecia grown on potato dextrose agar, both developed from the culture originally received from Harrison in 1935, have been deposited in the Plant Path. Herb., Cornell University under No. 23395. Duplicate specimens from this material have been deposited in the herbaria listed on p. 29.

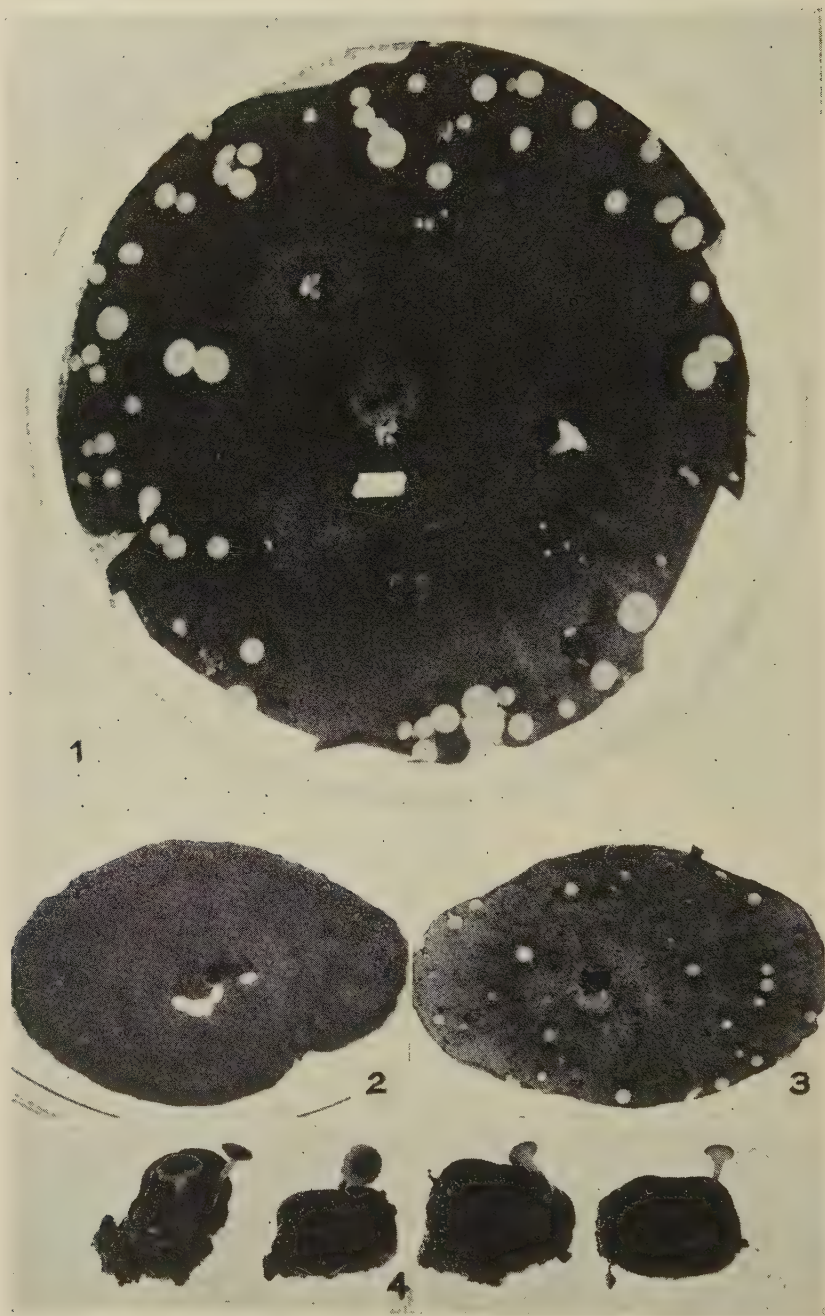


PLATE II. *Lambertella corni-maridis*.—Fig. 1. Apothecia from stroma produced on PDA, seven weeks after planting; apothecia matured on moist sand; 2, one of three mature stromata grown in

ILLUSTRATIONS: Harrison and El-Helaly, 1935, Text Figs. 1-4 and Pl. IV.

NOTES: This description while based primarily on the original by von Höhnelt and on the observations of Harrison and El-Helaly (1935) has been somewhat modified in conformity with my own studies on this species in culture.

The color of the apothecium varies considerably under different conditions. Harrison and El-Helaly (1935:201) say "flesh pink to pale brown." While speaking of the color in nature (p. 200) they say "some were pale pink to flesh colored, others buffy citrine (Ridgeway, Plate XVI), and others dark brown." Von Höhnelt (1918) says "Scheibe violettbraun, Excipulum blässer . . . Stiel, blass bräunlich, . . . an der Basis schwarz." Contrary to the statement of Harrison and El-Helaly (1935:201) I find the paraphyses to be normally three branched, not simple.

The stromata on PDA mature in about 14 days from planting (ascospores or mycelium) at 20° C. but apothecia do not develop thereon for about five or six weeks thereafter. My experience in this matter confirms that of Harrison and El-Helaly (1935:206) who report that "they appear about seven weeks from the date of inoculation."

✓ *Lambertella hickoriae* n. sp.

Pl. III and Text Fig. 2

Stroma consisting of pieces of hickory nut hulls that have been blocked off and preserved by the enveloping thin black rind. Medulla a loose hyphal network in which is enmeshed the partially digested hull tissues, the cells brown and contents disorganized. On PDA, diffuse, thin, discoid, covered during development with a rather profuse uniform wooly aerial mycelium. Rind pattern as in *L. corni-maris* (Text Fig. 1, c).

Spermatia develop abundantly on plain water agar in seven days at 21° C., not observed in nature; globose, 2-3 μ ; produced successively from the tips of clavate spermatophores in naked fasciculate spermodochia. This species is homothallic.

Apothecia arising from stromatized hickory nut hulls partially buried in the soil or leaf mold; av. 2 mm. in diameter, fleshy, stout-stipitate, elastic, fibrillose beneath, color variable, sayal brown or tawny olive to dark vinaceous brown; *disc* shallow saucer-shaped 1-4 mm.; *hymenium* olive brown or fuscous just before spore discharge, becoming lighter colored, sayal

same petri dish on PDA, about 20 days after planting; 3, one of three similar stromata with mature apothecia still in petri dish; 4, mature apothecia on mummied fruits of *Cornus mas*, artificially inoculated. All figures natural size. Note that food supply and environmental conditions markedly affect the size of the apothecia. The light color of the apothecial discs in figs. 1 and 3 is due to discharge of the brown spores just before the photograph was taken.

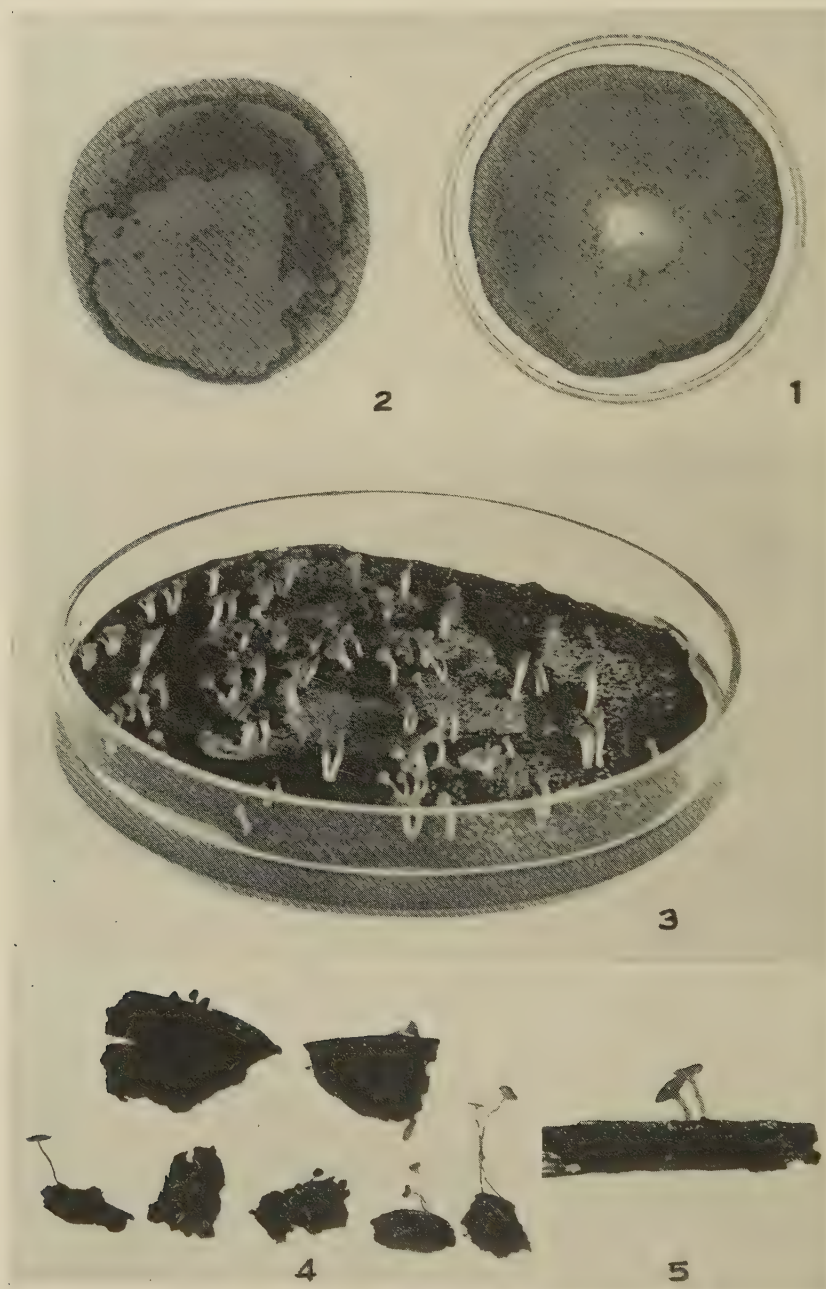


PLATE III. *Lambertella hicoloriae*. —Fig. 1. Upper surface of stroma on PDA. Note semi-floccose aerial mycelium and continuous upper rind; 2, under surface of same plate. Note discontinuous lower rind showing through the agar. Figures 1 and 2 half natural size; 3, apothecia developed from

brown or snuff brown immediately thereafter; *stipe* stout, elastic, light colored, avellaneous above, dark brown toward the base, fibrillose, hirsute. Apical cells of free hyphal tips swollen; *asci* cylindric-clavate, attenuate in the lower half, rounded or truncate and thickened at the apex, pore J+, $101-127 \times 6-8.4\mu$, mode $114.5 \times 7.2\mu$, av. 114.5×7.2 ; 8-spored, spores obliquely uniseriate, becoming biseriate; *ascospores* broadly elliptic, flattened

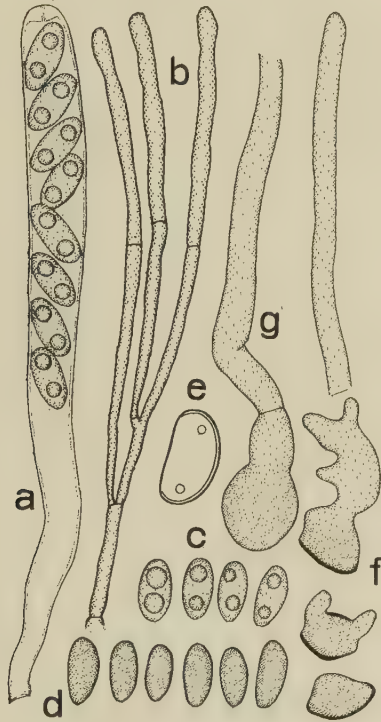


FIG. 2. *Lambertella hickoriae*.—*a*, Ascus containing young uncolored spores $\times 850$; *b*, paraphysis $\times 800$; *c*, young ascospores showing large guttulae $\times 850$; *d*, mature ascospores, guttulae masked $\times 850$; *e*, optical section of mature spore viewed from the side. Note thickening of convex face, and small guttulae $\times 1325$; *f*, three early stages in spore germination $\times 850$; *g*, germinated spore with long germ tube. Note the bulbous swelling of base of germ tube, ascospores, swollen greatly on germination $\times 850$.

on one side, wall thicker on the convex face, smooth, strikingly biguttulate and hyaline when young (guttulae J+), becoming olivaceous brown when mature, often discharged while still colorless, guttulae masked or disappear-

stroma grown on PDA, natural size; 4, apothecia from stromatized pieces of hickory nut hulls, original collection, natural size; 5, side view of apothecia developed on stroma from test tube slant on PDA, natural size.

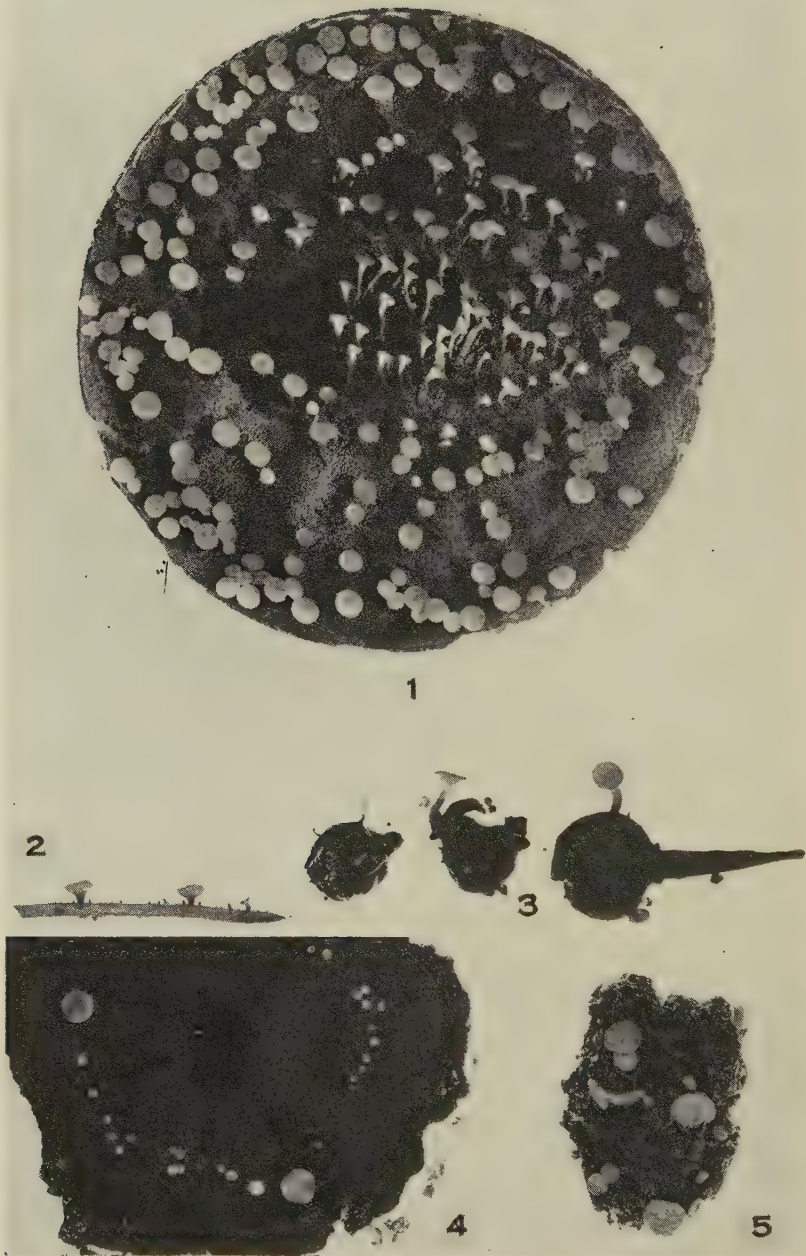


PLATE IV. *Lambertella jasmini* and *L. pruni*.—Fig. 1. Apothecia of *L. jasmini* on a stroma grown on PDA, three weeks after planting. Note heliotropic response of young apothecia, nat. size;

ing in the mature spores; two measurements of 50 spores each gave respectively, $7.8-10.4 \times 4.5-6.2\mu$, mode $9.1 \times 5.2\mu$, av. $9.2 \times 5.1\mu$; and $8.5-11.0 \times 4.5-6.5\mu$, mode $10.0 \times 5.2\mu$, av. $9.8 \times 5.2\mu$; *paraphyses* slender, two to four branched, septate, apical cells slightly clavate.

HABITAT: On stromatized hulls of *Carya ovata* (Mill.) K. Koch.

TYPE LOCALITY: Woods east of Cayuta Lake, New York, September 9, 1938.

DISTRIBUTION: Known only from the type locality.

TYPE SPECIMEN: Cornell University Pl. Path. Herb. 27881. Duplicate specimens have been deposited in the herbaria listed on p. 29.

NOTES: Abundant material of this species was first collected on September 9, 1938. The fungus has again been found in small quantities under the same tree in 1941. It can doubtless be found elsewhere within the range of its suscept.

Stromata develop and mature on potato dextrose agar in two to three weeks from date of planting with ascospores or mycelium. Mature apothecia develop in from 8 to 10 weeks from date of planting.

This species is very like *L. corni-marisi* in many of its characters. The ascospores of the two species are essentially alike in size, shape and color, the guttulae of *L. hicoriae* however disappear or are completely masked in the mature spores. The stipes of the apothecia are of a light avellaneous color in striking contrast to the dark vinaceous color of those of *L. corni-marisi*. It is in the developmental characters of their respective stromata on PDA that the two species are most readily distinguishable (See Pl. I).

Lambertella jasmini Seaver and Whetzel n. sp.

Pl. IV 1-3. Text Fig. 3

Stroma, a thin black subcuticular semi-stroma surrounding the mummified berries of *Jasminum* or irregular areas in the leaves delimited by a black rind layer which also spreads along over the leaf veins. Rind pattern typical of the genus (Text Fig. 1 c). On PDA thin, diffuse, discoid, continuous or interrupted, olivaceous brown, covered sparingly with fibrillose aerial hyphae.

Spermatia not observed. This species is homothallic.

Apothecia one to several arising from the stroma in fruits, pedicels or leaves of the suscept, 1-5 mm. in diameter, fleshy, stout-stipitate, elastic; *disc* shallow cupulate to applanate, at first chamois color to dark olive

2, section through a piece of the stroma bearing apothecial fundaments and mature apothecia, nat. size; 3, mummified berries of *Jasminum gracile*, bearing apothecia $\times 2$; 4, apothecia of *L. pruni* on a stroma produced on PDA, eight weeks after planting, nat. size; 5, stroma from sweet cherry fruit bearing apothecia $\times 2$.

buff, underside of receptacle concolorous with young hymenium, fibrillose, short tips of the hyphae forming a fringe about the margin of the cup; *hymenium* at first chamois color becoming buckthorn brown just before spore discharge, a pale Isabel color immediately thereafter; *stipe* stout to

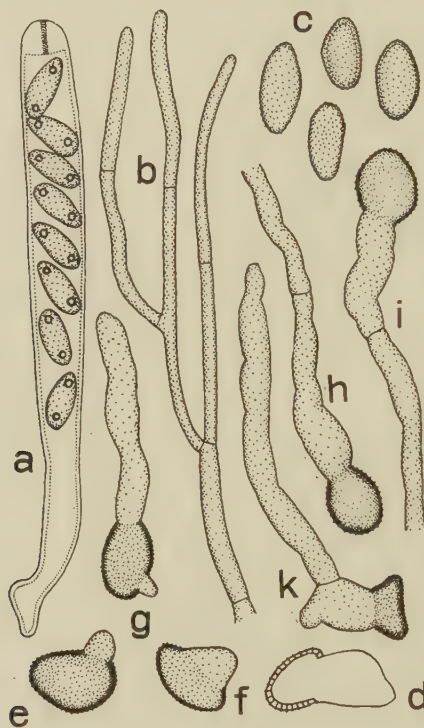


FIG. 3. *Lambertella jasmini*.—*a*, Ascus, containing young hyaline spores, showing the biguttulate condition and absence of wall ornamentation; *b*, three-branched paraphysis; *c*, four mature ascospores, thick walled with protruding ends of "wall plugs" showing $\times 1000$; *d*, diagrammatic section through germinating spore to show my concept of the "wall plugs"; *e-k*, stages in spore germination. The spores swell considerably on germination and the "wall plugs" become more prominent. The first cell adjacent to the spore is often markedly swollen. All figures except *c* $\times 900$.

slender, usually relatively short, above concolorous with receptacle, becoming darker with age, cinnamon brown, fibrillose, puberulent, with erect rather long spreading hairs abundant near the base, the apical cells of which are often swollen and prolonged into a slender apiculus. The apothecia of this species exhibit none of the vinaceous hue so characteristic of *L. corni-maris*, presenting instead a distinct yellowish coloration; *asci* cylindric, usually sharply attenuate in the lower third, forming a slender foot (Text Fig. 3a); apex rounded and thickened, pore faintly J+, 38 measurements $96.0-133.2 \times 7.2-9.6\mu$, mode $102.0 \times 7.3\mu$, av. $109.5 \times 8.3\mu$;

8-spored, spores uniseriate; *ascospores* broadly elliptic, flattened on one side, with peg-like thickening of a darker color than the rest of the wall (Text Fig. 3c) appearing as minute punctations or low warts over the surface, hyaline when young with two prominent guttulæ, becoming dark golden brown at maturity, 100 measurements $9.9-6.4\mu \times 5.3-3.2\mu$, mode $8.5 \times 4.6\mu$, av. $8.6 \times 4.2\mu$; *paraphyses* hyaline, slender, 2-3 branched, septate, apical cells slightly clavate.

HABITAT: On mummied berries and leaves of *Jasminum gracile* Andr.,⁶ and on leaves of *Citharexylum spinosum* L., Bermuda, November to January 1912, 1920, 1941, also isolated by J. M. Waterston, Bermuda Agr. Exp. Sta. from rotting fruit of the loquat, *Eriobotrya japonica* in May 1941.

TYPE LOCALITY: Walsingham, Bermuda.

DISTRIBUTION: Known only from Bermuda.

TYPE SPECIMEN: Cornell University Pl. Path. Herb. 29543 on berries of *Jasminum*, duplicate specimens of which have been deposited in the herbaria listed on p. 29, No. 29793 on fallen leaves of *Citharexylum spinosum* and No. 29437 on fruit of *Eriobotrya japonica* together with stromata and apothecia produced on potato dextrose agar from all three natural substrata are deposited in the Plant Path. Herb., Cornell University.

NOTES: The earliest collections of this species appear to be those of F. J. Seaver taken during the autumn of 1912 on mummied berries and leaves of *Jasminum gracile* (N.Y.B.G. Bermuda Explorations Nos. 1397 and 1362). These collections were very meager and are now of little value for study. It was collected again in January 1920 by Whetzel at Walsingham, Bermuda on the stromatized berries and leaves of the same suscept (Pl. Path. Herb. Cornell University Nos. 29479 and 29480) but again in very small numbers. This is the species referred to by Harrison and El-Helaly (1935:212). Both Seaver's and Whetzel's collections proving too scanty for a satisfactory description of the species, the assistance of J. M. Waterston, Pathologist of the Bermuda Experiment Station, was enlisted to obtain living material. During the late summer of 1941 he collected a large quantity of mummied berries of the Jasmine at Walsingham and sent them to me. Forcing them in moist chambers, a number of excellent apothecia developed from which a pure culture was obtained. Most of the mummied berries yielded a very similar appearing apothecial form which both Waterston and I had at first taken to be *L. jasmini* but which on critical examination proved to be a quite distinct hyaline spored stromatic discomycete. Earlier in the summer of 1941 the writer had received from Mr. Waterston a pure culture together with a small piece of the skin of a

⁶ Bailey (Gentes Herb. 4: Fasc. 9: Art. 29: 345. 1940) has shown that Britton was in error in referring this species to *J. simplicifolium* in his Flora of Bermuda p. 285, where he cites *J. gracile* Andr. as synonym.

rotting fruit of the loquat bearing a few apothecia of a brown-spored discomycete which was at once recognized to be a *Lambertella*. It had been thoroughly studied before the fresh apothecia and pure cultures were obtained from the mummied berries of Jasmine. A careful comparison of the two which have been grown and fruited simultaneously in pure culture leaves no doubt as to their identity. In November 1941 Waterston collected what proves to be the same species on fallen leaves of *Citharexylum spinosum*. Since the earlier collections of this species were made on berries of the Jasmine but are too scarce for critical study, the apothecial material developed at Ithaca, New York on berries from Bermuda is designated the *type* of this species.

That this fungus does invade and stromatize areas of the leaves of Jasmine is attested by examination of apothecia on a single leaf of my 1920 collection (Pl. Path. Herb. Cornell University No. 29479) and by my original notes made at the time of collecting. I have also received a leaf and twig of Jasmine from Mr. Waterston each showing stromata and apothecia of this species. The occurrence of this species in rotting fruits of the loquat is probably accidental rather than habitual. Its usual suspect is doubtless the Jasmine or *Citharexylum*. Its prompt development of apothecia in culture (2-3 weeks) from planting on potato dextrose agar in contrast to the relatively long period required for apothecial development by the other species (7 weeks to some months) is but one of several characters consonant with its tropical habitat. Its ability to thrive at and withstand relatively high temperatures is another. During the hot spell of 1941 (July and August) in the laboratory at Ithaca it grew rapidly and produced apothecia promptly while *L. corni-maritima* and *L. hickoriae* were seriously inhibited in their development.

✓ ***Lambertella pruni* Whetzel and Zeller, n. sp.**

Pl. IV 4-5 and Text Fig. 4

Stroma a thin, wrinkled black crust surrounding the mummied cherry, often adherent to the stone; on PDA a thin, diffuse zonate or discoid dull black crust formed at the surface above a submerged mat of ochre yellow mycelium; surface bare or covered with sparse white webby aerial hyphae; rind pattern typical of the genus (Text Fig. 1 c).

Spermatia globose, about 3-4 μ in diameter. Known only from agar cultures where they are produced in typical naked spermodochia. This species is apparently heterothallic.

Apothecia gregarious, as many as 100 arising from a single stromatized cherry at maturity 1.5 mm. diam., short stipitate to sessile, fleshy, elastic; *disc* from the first patellate to convex, white furfuraceous beneath, margin fringed with short hyphal tips, when young avellaneous to wood brown; *hymenium* pale buffy brown, becoming clove brown with maturity of the

ascospores, strikingly lighter colored immediately after spore discharge; *stipe* very short, sharply constricted at point of attachment; base black; *asci* long cylindric, slightly narrowed at the very tip, which is rounded and thickened, sharply attenuate at the base, pore J+; 25 measurements

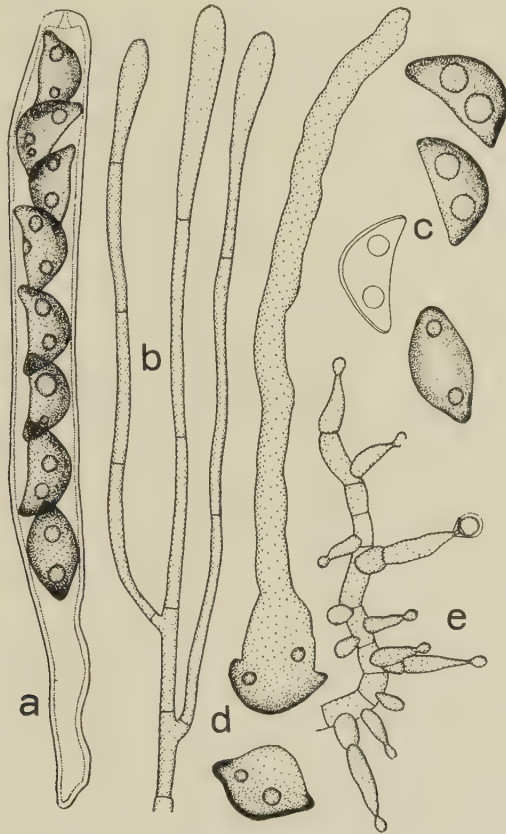


FIG. 4. *Lambertella pruni*.—*a*, Mature ascus with spores ready for ejection; *b*, paraphysis; *c*, mature ascospores, the two above in side view, the lowest in concave face view, the fourth in a diagrammatic optical section showing thickening of convex face $\times 1000$; *d*, two stages in germination of the spore; *e*, early stage in development of the spermodochium. All drawings, except *c*, $\times 880$.

$115-150 \times 10-14\mu$, mode $126 \times 11\mu$, av. $126 \times 12\mu$; 8-spored, spores uniseriate; *ascospores* lunate, with broad blunt ends, the convex wall thick and dark, the concave wall thin and light colored, smooth, biguttulate, guttulae J+, golden brown becoming dark olivaceous brown at maturity; 50 meas. $12-18 \times 7-8.4\mu$, mode $14 \times 8.4\mu$, av. $15 \times 8\mu$, germ tube arising from the thin concave face; *paraphyses* three-branched, septate, apical cells more or less clavate and vacuolate.

HABITAT: On mummied fruits of the sweet cherry, *Prunus avium* and seedlings of same (Mazzard).

TYPE LOCALITY: Reynold's Estate near Salem, Oregon, March 13, 1941.

DISTRIBUTION: Known only from the type locality.

TYPE SPECIMEN: Cornell University Pl. Path. Herb. 29100 collected by A. W. Evans and S. M. Zeller on March 13, 1941. This material is too scanty to divide, but apothecia developed on cherry mummies collected by Zeller and Evans in February 1942, Cornell Univ. Pl. Path. Herb. No. 29378, have been distributed to the herbaria listed on p. 29.

NOTES: This species was discovered by A. W. Evans in mid-April 1940. Evans and C. E. Owens secured a small collection at that time. On April 16 of that year Dr. C. E. Owens sent me, in a liquid preservative, two cherry mummies bearing apothecia. As such material of discomycetes is of little value for microscopic examination these were washed in water, dried and put in our herbarium under No. 29699.

From dried specimens of the 1940 collection which Dr. Zeller had sent to Dr. F. L. Drayton of the Dominion Experimental Farms, Ottawa, Canada and which later Drayton sent to me, I readily obtained, by dilution plates in acid PDA ten months after they had been collected, nearly 100% germination of the ascospores. From these plantings I obtained ascospore isolates which grew very rapidly, forming apparently mature stromata in about fourteen days. Stromata removed from the agar and placed in a moist chamber on sand produced mature apothecia in about 7 to 8 weeks from the date of planting on agar. Unlike the other six species grown in the laboratory, *L. pruni* has produced apothecia very sparingly for me and only from stromata developed from mass ascospore plantings. Drayton (letter of April 17, 1942) reports development of mature apothecia from plantings of single asci (8 spores) in two cases while a single ascospore isolate made at the same time produced no apothecia. His cultures planted December 23, 1941 on PDA were carried in total darkness at 14°C. The mature apothecia were discovered April 17, 1942, nearly 4 months after date of planting. The long time taken by Drayton's culture to produce mature apothecia was probably due to the absence of light. The low temperature at which they were grown may also have retarded apothecial development since I have found that a temperature of 18°-21° appears to be optimum for growth and development of the stromata of this species.

Sweet cherry mummies collected by Zeller, Feb. 19, 1942, and received by me (dry) on Feb. 27, were found when moistened to be already studded with numerous apothecial fundaments and young, nearly fully expanded apothecia but showing no ripe ascospores. Placed on moist sand in a preparation dish many of these apothecia contained mature ascospores by March 6. Thus in the orchard in late March when the apothecia of this species may be already mature and discharging spores, the sweet cherry

trees are in the "pre-blossom or delayed dormant spray stage." The apothecia are all "gone by full bloom of the trees" (Zeller letter of Feb. 20, 1942). It is difficult to explain how this fungus bridges the period from final ascospore discharge until well developed or mature fruits appear. No blossom infection has been observed and there is no conidial stage. That the ascospores may germinate and the fungus vegetate in the soil until ripe fruits fall is possible but would be most unusual for discomycetes of this type.

This species in its vernal fruiting habit is in striking contrast to the other species of *Lambertella* which produce their apothecia in late summer or autumn or in the tropics at such times as their natural substrata are mature or maturing. The relatively long period between stomatal formation and apothecial production is probably the result of the overwintering habit as in the case of *L. corni-maris* and *L. hicoriae*.

Certain striking features of *L. pruni* deserve being stressed. The ascospores are remarkable in their shape and manner of germination (Text Fig. 4) being quite distinct in these respects from the spores of the other species. Their remarkable retention of vigorous vitality under dry conditions is apparently unusual. The production of ochre yellow pigment in culture on PDA, while occurring in all species of *Lambertella* thus cultivated, is in no other nearly so profuse as in *L. pruni*. This pigment forms clusters of slender crystals in the surrounding medium. These turn purple and slowly dissolve in KOH. The sessile or very short stipitate habit of the apothecia is a character which in this species appears to be little affected by environmental factors such as light and the humidity of the air.

***Lambertella viburni* n. sp.**

Pl. V and Text Fig. 5

Stroma, a subcuticular network of fairly broad irregular black bands following the veins of the leaf (Pl. V 1 and 2). Stomatization restricted largely to the veins, with occasional black lines blocking off small areas of the blade. The rind surrounds the veins, the pattern typical of the genus (Text Fig. 1 c). On potato dextrose agar the stroma is thin, diffuse, olivaceous brown, covered at first with a sparse white pruinose to floccose coating of aerial hyphae, at maturity bald.

Spermatia globose, borne in tiny lenticular black spermogonia which are formed under the cuticle adjacent to the stroma as described by White (1941:221) for *Rutstroemia pruni-serotinae*. This species is homothallic.

Apothecia scattered, arising from the stroma, small, 0.5-2 mm. diam., fugacious; *disc* shallow saucer-shaped to applanate, fibrillose beneath, light buff, margin dark brown, incurved, rimmed with hyphal tips; *hymenium* mummy brown just before spore discharge, ochraceous tawny immediately



PLATE V. (See opposite page for explanation.)

after; *stipe* stout, cinnamon brown, concolorous throughout or lighter above, hirsute with tangled erect hyphae; *asci* slender, cylindrical, tapering slightly below, apex rounded and thickened, fugacious, pore J+, immature asci, 25 meas. $60.0-114.0 \times 7.5-9.7\mu$, mode $108.0 \times 9.0\mu$, av. $97.8 \times 8.8\mu$; 8-spored, spores usually biseriate in upper half of the long ascus; *ascospores*

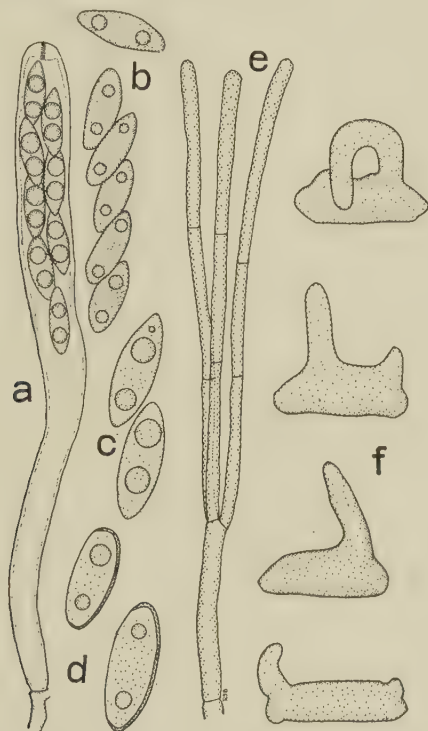


FIG. 5. *Lambertella viburni*.—a, Ascus with small, young, uncolored, pointed spores $\times 875$; b, ripe ascospores $\times 875$; c, full sized uncolored spores $\times 1325$; d, optical section through fully ripened ascospores, showing thickened darker band about convex face $\times 1325$; e, fasciculate paraphysis $\times 875$; f, early stages in germination of young uncolored ascospores. The spores in this species are usually discharged before showing much if any coloration.

long ellipsoid, bluntly apiculate, flattened on one side, light brown with darker band about convex side of the spore, becoming fully colored only after they are discharged, biguttulate, 100 measurements (oil immersion) $11.7-18.0 \times 4.0-6.0\mu$, mode $13.5 \times 5.0\mu$, av. $13.5 \times 5.0\mu$; *paraphyses* appar-

PLATE V. *Lambertella viburni*.—Fig. 1. Leaf of *Viburnum cassinoides* showing stromatized veins and young apothecia near the tip $\times 2$; 2, a portion of the upper right tip of the blade greatly enlarged, showing four young apothecia. Note the black rind along the upper side of the stromatized veins and the lighter colored areas with groups of minute black spermogonia $\times 4$; 3, apothecia from stroma produced on PDA, nat. size.

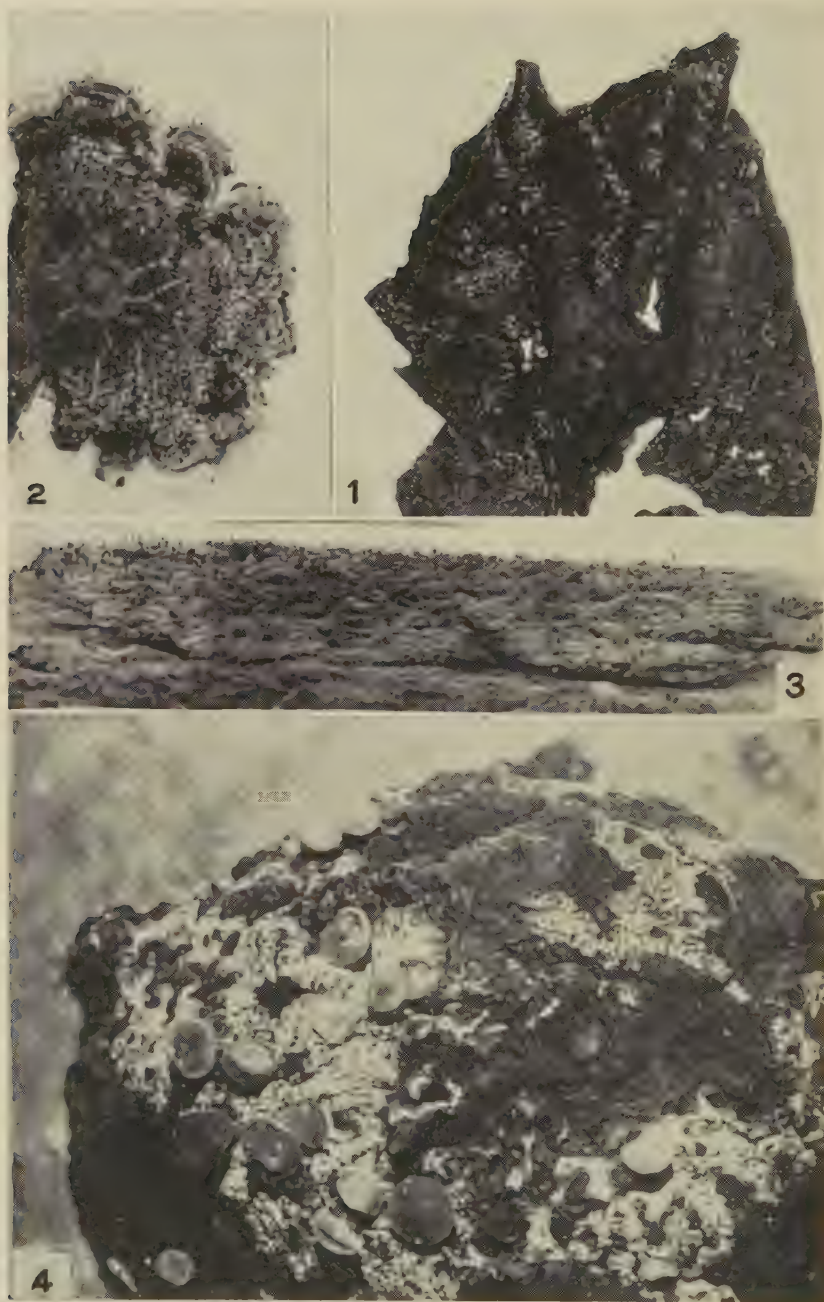


PLATE VI. (*See opposite page for explanation.*)

ently simple, actually fasciculately three-branched near the base, septate, slightly enlarged toward the tip.

HABITAT: On hanging dead leaves of *Viburnum cassinoides*.

TYPE LOCALITY: The "Bottomless Pit" near Hanover, New Hampshire, August 27, 1937.

DISTRIBUTION: Known only from type locality.

TYPE SPECIMEN: Cornell University Pl. Path. Herb. 26906. Because of the small amount of material available duplicates have not been distributed to other herbaria.

NOTES: The hanging dead overwintered leaves were apparently killed the previous season by some insect boring in the twigs. Small, short-lived apothecia, deliquescent asci and the slender spores becoming colored after discharge are the striking characters of this species.

✓ *Lambertella cephalanthi* n. sp.

Pl. VI and Text Fig. 6

Stroma. No distinct stromatization of the invaded leaves has been detected. When first isolated on potato dextrose agar stromata with rind pattern typical of the genus were formed. After several transfers a distinct stroma failed to develop.

Spermatia not observed. This species is homothallic.

Apothecia scattered, arising from the surface of the leaf, minute 0.16–1.0 mm. diam.; *disc* deeply cupulate to applanate, margin fringed with short hyphal tips, clay colored when young; *hymenium* dark smoke brown just before spore discharge, becoming clay colored immediately thereafter; *stipe* dark brown below, above concolorous with and pruinose like the under-side of the cup; *asci* short, stout, broadly cylindrical, tapering slightly to the base, abruptly narrowed at top, apex rounded, more or less truncate, pore conspicuously J+; 40 meas. $90-117 \times 10.5-12.0\mu$, mode $102 \times 12\mu$, av. $100 \times 11\mu$; 8-spored, spores uniseriate becoming biseriate, nearly filling the entire ascus; *ascospores* broadly ellipsoid, olivaceous brown with thickened darker band about one side, distinctly biguttulate even at maturity, 100 measurements from the type collection (oil immersion) $11.7-16.9 \times 5.2-7.8\mu$, mode $13.6 \times 6.5\mu$, av. $13.6 \times 6.5\mu$; *paraphyses* three-branched, septate, tips distinctly swollen.

HABITAT: On fallen leaves of *Cephalanthus occidentalis*.

TYPE LOCALITY: West Roxbury, Mass., August 21, 1936 (C. U. Pl. Path.

PLATE VI. *Lambertella cephalanthi* and *L. colombiana*.—Fig. 1. Upper half of leaf of *Cephalanthus occidentalis*, upper surface showing 3 tiny apothecia $\times 2$; 2, stroma of *L. cephalanthi* grown on PDA nat. size; 3, apothecial fundaments on stroma of *L. cephalanthi*, grown on PDA nat. size; 4, apothecia of *L. colombiana* arising from crust-like stroma on nut $\times 4$. Courtesy Miss Edith Cash.

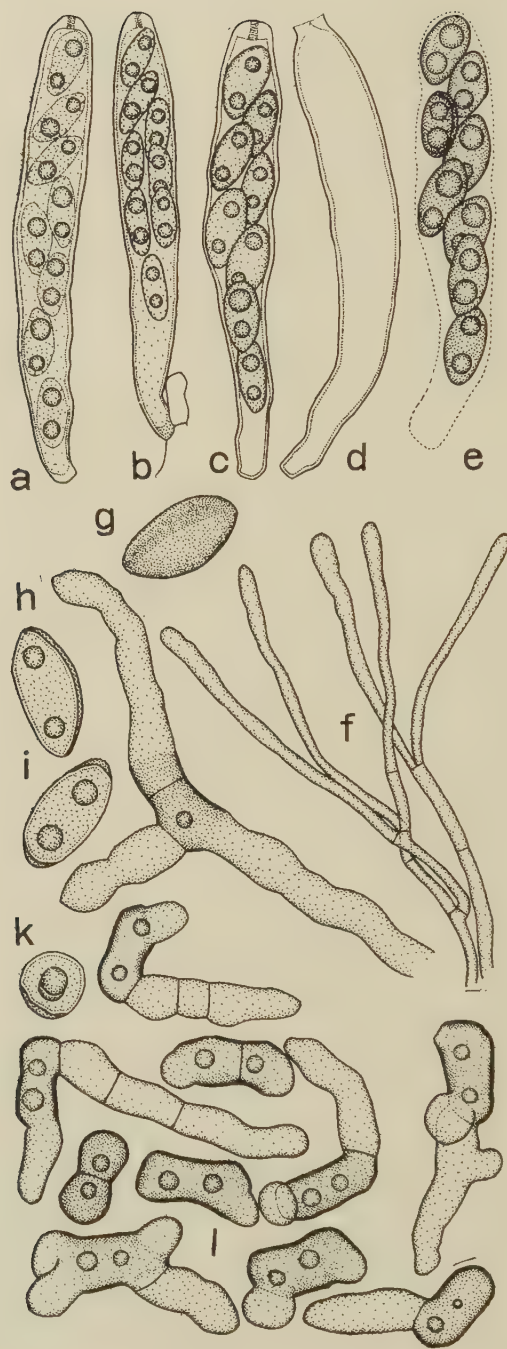


FIG. 6. (See opposite page for explanation.)

25514). Also collected in a swamp at Cayuta Lake outlet, New York, September 1, 1936 (C. U. Pl. Path. 25526).

DISTRIBUTION: Known only from the type locality and from swamp at outlet of Cayuta Lake, New York.

TYPE SPECIMEN: Cornell University Pl. Path. Herb. 25514 and Farlow Herbarium. Owing to the small amount of material available duplicate specimens have not been deposited in other herbaria.

Lambertella tropicalis (Kanouse) n. comb.

Text Fig. 7

Ciboria tropicalis Kanouse, Mycologia 33: 463. 1941.

Revised description based on dried material only.

Stroma subcuticular, in surface view an irregular area along the midrib and side veins of the leaf, blocked off by a thin black rind extending at right angles through the blade from upper to lower surface. The enclosed stromatized area consisting of a loose network of hyphae enmeshing the partially digested and preserved leaf tissues. This stromatic area is of a different color and firmer texture than the surrounding uninvaded leaf tissues. The black rind line delimiting the invaded area is inconspicuous in the dry leaf except under a binocular.

Spermatia ellipsoid, about $2.5 \times 1.5\mu$ borne in minute, black lenticular spermogonia formed beneath the cuticle in the stromatized area (Text Fig. 7b).

Apothecia scattered over the stromatic area on the upper surface of the leaf, small, 2 mm. diam., very short stiped, nearly sessile, stout, tough, waxy, white when fresh, pale alutaceous when dry, minutely furfuraceous beneath, concolorous throughout except for a tinge of brown beneath; *disc* applanate; *stipe* very short, and thick; *asci* cylindric-clavate, broadest at the apex, tip rounded and thickened, pore J+, $90-110 \times 8-11\mu$, 8-spored, spores uniseriate or irregularly biseriate, almost completely filling the ascus; *ascospores* inequilateral, slightly allantoid, fully formed spores still in the asci hyaline or slightly colored, $11-14 \times 4-5\mu$, contents finely granular, no guttulae evident, at maturity "golden brown" (?); *paraphyses* filiform, apparently simple, actually, however, 2-3 branched, branches easily detached, septate.

HABITAT: Leaves of *Coccolobis* sp. (?).

FIG. 6. *Lambertella cephalanthi*.—*a*, Ascus with spores just delimited; *b*, young ascospores, walls hyaline; *c*, ascospores light brown, not fully ripened but ready to be discharged; *d*, empty ascus; *e*, fully ripe spores, undischarged, ascus wall deliquescent; *f*, paraphyses; Figures *a-f* $\times 830$; *g*, surface view of convex face of spore showing thickened, dark band in wall; *h*, optical section of spore, side view; *i*, optical section seen from flattened face; *k*, optical section, end view. Figures *g-k* $\times 1285$; *l*, various forms and stages in germinating ascospores $\times 830$. In this species the germinating spore occasionally becomes septate.

TYPE LOCALITY: El Cayo Dist., Valentin, British Honduras, June 24, 1936, E. B. Mains.

DISTRIBUTION: Known only from the type locality.

TYPE SPECIMEN: This consists of a single dead leaf of what appears to be a species of *Coccolobis*. This is deposited in the herbarium of the University of Michigan under the label "Plants of British Honduras" (3582). Microscopic mounts of the stroma, spermogonia, asci, etc., are deposited

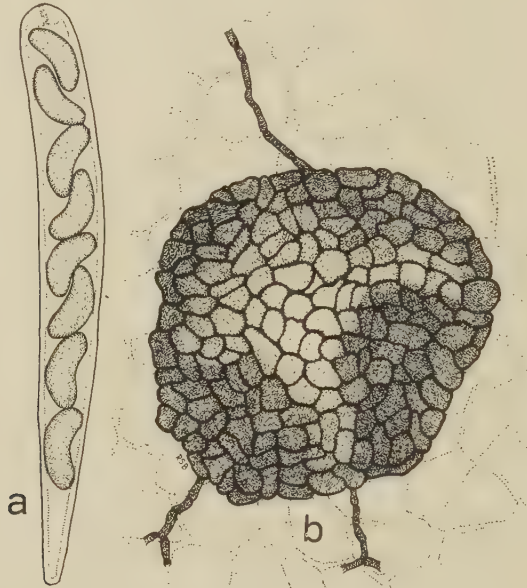


FIG. 7. *Lambertella tropicalis*.—a, Ascus with mature spores $\times 850$; b, spermogonium as seen from above, sub-cuticular, $\times 950$.

in the herbarium of the Dept. of Plant Pathology, Cornell University, under the No. 29677.

NOTES: If *Ciboria caucis* (Rebent.) Fckl. be accepted as the type of the genus *Ciboria*, this species cannot properly be referred to that genus. The character of the stroma, the form and color of the ascospores and the color and structure of the apothecia is quite different from these organs in the true *Ciboria* species. There may be some question of the transfer of this species to the genus *Lambertella*. In the characters of its stroma, spermogonia and apothecia it strikingly parallels *L. viburni*, from which species it is, however, undoubtedly distinct. If its mature ascospores are "golden brown" as my observations on the very limited material at my disposal leads me to believe, it is certainly congeneric with the other *Lambertella* species as I now conceive that genus. Dr. Kanouse noted "golden brown" spores in certain of her preparations but "was not able to connect the free

floating colored spores"⁷ with the apothecia she examined. I too found a few "golden brown" spores of the correct shape and size lying free on the leaf about the apothecia. I also found distinctly yellowish brown ascospores still in the asci in a mount from one of the two apothecia examined. That the asci and ascospores as described by Dr. Kanouse were immature is, I think, certain. In the mounts I have studied from two apothecia ejected spores were not to be found. They certainly would have been had any of the spores been fully mature. Future collections and cultures of this most interesting species can alone settle beyond question whether this fungus is or is not a true *Lambertella*. The stroma and spermogonia which are not recorded by Dr. Kanouse are clearly discernible under the binocular microscope. The apothecia are borne on the upper surface of the leaf, not on the underside as stated in the original description.

***Lambertella colombiana* Cash and Whetzel n. sp.**

? *Lambertella* sp. Cash, Edith K., Univ. Iowa Studies in Nat. Hist. 17: 213. 1937.

Pl. VI 4

Emended description.:—*Stroma* a well developed thin, black crust over those portions of the substrate from which the apothecia arise; the surface rind and the submerged rind both one cell thick, of a dark olivaceous-black color; rind pattern typical of the genus; medulla a dark brown amorphous mass resulting from the partial disintegration of the susceptible tissues and threaded throughout with hyaline, branched hyphae connecting the two rind layers.

Spermatia not observed.

Apothecia gregarious, small 1–2 mm. diam., arising from the stromatic crust, short stipitate to nearly or quite sessile, fleshy coriaceous, color in fresh condition unknown, on drying they turn Prout's brown to fuscous black; *disc* patellate, becoming convex, margin fimbriate with a few delicate threads of pale brown; *asci* cylindrical, rounded and thickened at the apex, gradually narrowed toward the base, pore J+, 90–110 × 7μ, 8-spored, spores uniseriate; *ascospores* ellipsoid, slightly flattened on one face, olivaceous brown, wall thicker on the convex face, biguttulate, 11–13 × 4–6μ; *paraphyses* filiform, three-branched near the base, slightly enlarged toward the apex to about 3μ.

HABITAT: Stromatized hulls of a nut of unknown identity.

TYPE LOCALITY: The Sierra Nevada de Santa Marta, Cerro Quemado trail, Colombia, altitude above 1500 M. August 26, 1935. Coll. G. W. Martin.

DISTRIBUTION: Known only from the type locality.

TYPE SPECIMEN: The material consisting of a single nut, now somewhat

⁷ Letter of February 16, 1942.

broken up, is deposited in the herbarium of the University of Iowa, Iowa City, Iowa (3761). Microscopic mounts are also deposited in the herbaria of the Division of Mycology and Plant Disease Survey, Bu. Pl. Ind., Washington, D. C. and of the Dept. of Plant Pathology, Cornell University, Ithaca, New York, 31506.

NOTES: This species, first described by Miss Cash in 1937, and referred by her doubtfully to the genus *Lambertella* without giving it a specific name, has now been critically restudied in comparison with the other species of *Lambertella* here described. As a result we have no hesitation now in placing it definitely in *Lambertella* and join in naming it for the country in which it was discovered.

A bit of the black crust from which the apothecia arise after soaking for some days in weak KOH solution, proves to be a well developed stroma, showing the rind pattern so characteristic of all species in this genus (Text Fig. 1 c). The paraphyses were found to be branched instead of simple, and the ascospores thickened and darker colored on the convex face, a character which seems to be of more or less generic significance.

Made hopeful by the readiness with which ascospores of *L. pruni* from apothecia dry for nearly a year had germinated, dilution plates of spores of *L. colombiana* in acid PDA were also poured but not a single spore germinated. While they may be long lived in the dry condition, six years is apparently too much for them. I have thus, unfortunately been unable to see and study this species in pure culture. It is hoped that mycologists collecting in the American tropics will be on the alert for this species since it will undoubtedly grow readily on culture media and being a tropical species will very likely fruit in a very short time as is the habit of *L. jasmini*.

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On the Taxonomy of the Genus *Encopognathus* (Hymenoptera: Sphecidae: Pemphilidini)

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In 1896 Kohl, in his classic paper "Die Gattungen der Sphegiden,"¹ proposed *Encopognathus*² as an "Artengruppe" (*i.e.*, subgenus) of the "Haupt-Artengruppe" *Lindenius*, basing it upon a unique female from Senegambia. For the following four decades, during which a number of African, Mediterranean and Oriental forms were added to it, *Encopognathus* was believed to be confined exclusively to the Old World. But in 1936 I recorded its presence definitely in the western hemisphere, raising the entity then to full generic rank³ and establishing a discrete subgenus, *Rhectognathus*,⁴ for the reception of the Nearctic form *E. pectinatus*. This, however, as I have since discovered, was not the first North American *Encopognathus* described. For in 1921 Banks characterized from the Lake Tahoe region in California a *Lindenius wenonah*⁵ which, as an examination of the type in the Museum of Comparative Zoölogy has revealed, is indubitably an *Encopognathus*. Although Banks' *wenonah* is referable to the present genus, it forms a distinct group therein, separate and discrete from *Rhectognathus* as indicated on the following pages. In view of this, and inasmuch as I have now before me, as I did not in 1936, African representatives of typical *Encopognathus*, through the courtesy of Dr. George Arnold, Director of the National Museum of Southern Rhodesia, and Captain R. H. R. Stevenson, both of Bulawayo, Southern Rhodesia; and Oriental material from Mr. Nathan Banks, Curator of Insects at the Museum of Comparative Zoölogy in Cambridge, I offer here a review of the interesting myrmecotherous genus *Encopognathus*. To Dr. P. H. Timberlake of the Citrus Experiment Station at Riverside, California, I express my thanks for his courtesy in sending for examination and study the type of his species *Encopognathus (Rhectognathus) rufiventris*.

Encopognathus Kohl

- Crabro (Encopagnathus)* Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XI, p. 486 (1896).—Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XXIX, p. 320 (1915).
Thyreopus (Lindenius species-group Encopognathus) Arnold, Ann. Transvaal Mus., XI, pp. 340, 345 (1926).
Encopognathus Ashmead, Canad. Entom., XXXI, p. 166 (1899).—Pate, Ent. News, XLVII, pp. 150–153 (1936).—Pate, Mem. Amer. Ent. Soc., no. 9, p. 25 (1937).

¹ Kohl: Ann. k. k. Naturhist. Hofmus. Wien, XI, pp. 233–516 (1896).

² Kohl: Ann. k. k. Naturhist. Hofmus. Wien, XI, p. 486 (1896).

³ Ashmead in 1899 was actually the first to accord *Encopognathus* full generic rank. Cf.: Canad. Entom., XXXI, p. 166 (1899).

⁴ Pate: Ent. News, XLVII, pp. 147–153 (1936).

⁵ Banks: Ann. Ent. Soc. Amer., XIV, p. 16 (1931).

GENOTYPE: *Crabro* (*Encopognathus*) *Braueri* Kohl, 1896 [= *Encopognathus* (*Encopognathus*) *braueri* (Kohl)]. (Monobasic.)

In common with *Entomognathus* and the Neotropical entity *Entomocrabro*, both sexes of *Encopognathus* have the mandibular apices simple and the inferior margins deeply excised, and the ultimate abdominal tergite provided with a distinct pygidial area. The naked eyes serve as the most obvious feature for differentiating *Encopognathus*, and *Entomocrabro* as well, from *Entomognathus*. But in *Entomognathus* the anal lobe of the hind wing is longer than the short submedian cell, while the transverse cubital vein of the fore wing is straight, oblique, and received on the radial vein beyond the middle of the marginal cell, whereas in *Encopognathus* the anal lobe is at most subequal in length to the submedian cell of the hind wing and the transverse cubital vein of the fore wing is sharply angulate medially, or at least strongly sinuate, and received by the radial vein at or before the middle of the marginal cell.

The chief features distinguishing *Encopognathus* from the interesting Neogaenic entity *Entomocrabro* have been presented elsewhere in a review of that genus.⁶

Generic Characters.—More or less compact, small forms. Head suborbicular to subquadrate in anterior aspect, transversely subrectangular in dorsal aspect; eyes naked, reaching to bases of mandibles, the malar space therefore wanting; front without a marginate scapal sinus; ocelli situated in a low isosceles triangle or curved line. Maxillary palpi with six, labial palpi with four segments. Mandibles with apices simple and acuminate in both sexes; the lower margins deeply excised medially.

Thorax robust. Pronotum short, transverse, linear, situated more or less on a level with the mesonotum. Propodeum short; dorsal surface usually with a more or less distinct trigonal area discally.

Legs relatively robust. Middle tibiae with a small apical calcar in both sexes; hind tibiae with two rather large and distinct calcaria. Females usually with a pecten on fore tarsi.

Fore wings with marginal cell rather long, and broadly and either squarely or somewhat obliquely truncate at apex, furnished there with a large and distinct appendiculate cell usually open apically; transverse cubital vein joining radius at about middle of marginal cell, and usually distinctly and sharply angulate medially: the anterior (upper) ordinate straight and perpendicular, and the posterior (lower) ordinate oblique and sharply inclined toward distal end of cubitus; recurrent vein received about on middle of cubitus but not causing the latter to be appreciably angled backward; first discoidal cell trapezoidal. Hind wing with the submedian

⁶ Cf. Pate: *Revista de Entomologia* (Rio de Janeiro), XII, p. 46 (1941). *V. et.*: *Ent. News*, XLVII, pp. 50-53 (1936).

cell usually short, the anal lobe shorter than, or at most subequal to it (except in *Aryana*).

Abdomen sessile. Tergites folded roundly under and imbricate with the convex sternites; intermediate tergites usually with basal acarid chambers.⁷ Ultimate tergite of both sexes with a distinct pygidial area. Males with the apical sternites simple, unmodified.

Subgenera.—The build of the species comprising the present genus is quite diversified. A detailed and critical analysis of the diagnostic attributes of the component species indicates the existence within *Encopognathus* of two distinct phyletic lines,—one in each hemisphere.

The New World forms are an aggregation of finely punctate species with the mesopleura lacking both an epicnemium anteriorly and vertical carinae before the middle coxae; the axillae simple and immarginate laterally; the propodeum finely sculptured and devoid of lateral carinae; the vertex without supra-orbital foveae; the occipital carina incomplete and not attaining the hypostomal carinule bordering the oral fossa; and the abdomen more or less depressed. In sharp contrast to these are the coarsely punctate Old World forms which have the mesopleura furnished with a distinct epicnemium anteriorly and sharp vertical carinae before the middle coxae as well, while the axillae are large, prominent, and sharply margined laterally; the propodeum more or less coarsely areolate and provided with well developed lateral carinae; the head with distinct supra-orbital foveae; the occipital carina complete and reaching the hypostomal carinule, and the abdomen cylindrical in cross section. These forms of the eastern hemisphere give every indication of being specializations of, or developments from, an ancestral stock similar to or identical with that now exemplified by the simpler, more primitive, extant New World species. The latter may then be regarded as relict forms that have been pushed out into peripheral areas, isolated and left stranded in western North America and southwestern Europe by a more vigorous, rapidly evolving and centrally located stock which has eventually developed into the distinctive groups now found in India and the Ethiopian Region.

Each of these major lines of development within *Encopognathus* is in turn separable into two distinct phylogenetic lines. Inasmuch as these four groups give every appearance of being natural entities, I have chosen to regard them as discrete subgenera. Recently Timberlake has expressed the opinion that the Californian group, for which I proposed the name *Rhectognathus* several years ago, merits recognition as a distinct genus.⁸ In view

⁷ These are present in most of the various groups of the Pemphilidines, but are usually more or less concealed by the overlapping, caudal margins of the preceding tergites. In many of the larger forms, mites are often found congregated there, and these transverse basal pockets, invaginations or folds on the abdominal tergites may therefore be interpreted as acarid chambers.

⁸ Timberlake: Ent. News, LI, p. 167 (1940). At the present juncture, I see no reason for be-

of the congeries of characters wherein the New and Old World forms differ from each other, there is some justification for this belief. However, since the venation and other basic characters of *Rhectognathus*, and now its New World kin *Tsaissuma* as well, are identical with, or so similar to, those displayed by *Encopognathus* in the restricted sense, I prefer at present to regard *Rhectognathus* as merely a subgenus.

The subjoined table will serve to differentiate the several subgenera of *Encopognathus* recognized here.

KEY TO THE SUBGENERA OF ENCOPOGNATHUS

1. Mesopleura with a sharp epicnemium anteriorly, and with a vertical carina before middle coxae; vertex with supra-orbital foveae; occipital carina attaining hypostomal carinule bordering oral fossa; pronotum with dorsal surface transversely carinate anteriorly; axillae with lateral edges sharply margined; propodeum with lateral carinae present and well developed; abdomen not depressed; females without a psammophore; coarsely punctate Old World forms. 3
- Mesopleura rounded, without a sharp epicnemium anteriorly, and without a vertical carina before middle coxae; vertex without supra-orbital foveae; occipital carina incomplete, not attaining hypostomal carinule; pronotum rounded, without a complete transverse carina anteriorly on dorsal surface; axillae with lateral margins rounded; propodeum without trace of lateral carinae; abdomen more or less depressed; females with a psammophore; finely punctate New World forms. 2
2. Antennae of males with thirteen, of females with twelve segments, the antennal sockets subcontiguous to lower inner orbits; abdominal tergites without evident basal acarid chambers; male fore tarsi patellate. *Tsaissuma* new subgenus
- Antennae of both sexes twelve-segmented, the antennal sockets well separated from lower inner orbits; abdominal tergites with well developed basal acarid chambers; male fore tarsi simple or distorted but not patellate. *Rhectognathus* Pate
3. Mesopleura distinctly separated from mesothoracic epipleura; hypersternauli present; head with posterior orbits not margined by a carinule, and antennal sockets relatively remote from lower inner orbits; fore wing with transverse cubital vein oblique, sinuate, but not sharply angulate medially; hind wing with submedian cell long, the anal lobe only about one-half its length; males with antennae thirteen-segmented; Oriental and Eremian forms.
- *Aryana* new subgenus
- Mesopleura ankylosed with epipleura; hypersternauli absent; head with posterior orbits margined by a carinule, and antennal sockets subcontiguous to lower inner orbits; fore wing with transverse cubital vein distinctly angulate medially; hind wing with submedian cell short, the anal lobe subequal in length to it; both sexes with antennae twelve-segmented; Ethiopian forms. *Encopognathus* Kohl

ETHOLOGY

Relatively little is known about the biology of the members of this genus. García Mercet states he has encountered *Encopognathus braunsi* flying during the months of May and June over sandy areas exposed to the sun in the neighborhood of rivers and arroyos near Madrid, Spain, and that like many other Sphecoid wasps it nests in the soil.⁹ Arnold has found that *Encopognathus chiridensis* preys upon ants,¹⁰ and also records that Captain

lieving any affinity, even remote, exists between *Rhectognathus* and the Miscophine genus *Bothynostethus*, as Timberlake tentatively suggests. His point, however, is interesting and well taken.

⁹ García Mercet: Bol. R. Soc. Españ. Hist. Nat., XV, pp. 369-370 (1915).

¹⁰ Arnold states (1932), Occ. Pap. Rhodesian Mus., no. 1, p. 19) that *E. chiridensis* was ob-

R. H. R. Stevenson has observed *E. browni* nesting in sandy banks at Rhodesdale in Southern Rhodesia.¹¹

The females of the subgenus *Rhectognathus* possess a well developed psammophore,¹² consisting of mandibular, temporal, coxal, trochanteral, femoral and tibial ammochaetae, and this is presumptive evidence that they, like their South African and European congeners, nest in dry, sandy or friable soil, and excavate their burrows in a manner comparable to that of *Belomicrus* and *Anacrabro*.¹³ But it is curious that none of the Old World forms have developed a psammophore. This fact lends additional support to the recent contention of Timberlake that *Rhectognathus* merits recognition as a discrete genus.¹⁴

DISTRIBUTION

The distribution of the genus *Encopognathus*, as known at present, is discontinuous, and parallels in certain respects that displayed by *Belomicrus*.¹⁵ Like that Oxybeline genus, *Encopognathus* is confined largely to the warmer, more xeric areas of the earth, with three Nearctic representatives known at present from California, one from central Spain in the Palaearctic Region, three Oriental forms in India, and six species in South Africa. Further collecting in, and intensive study of, material from western North America, the Mediterranean and Eremian areas of the Palaearctic Region, and the xeric Sudanese, Somali, and East African provinces of the Ethiopian Region will doubtless reveal additional new forms in the fauna of, or at least result in the extension of the genus to, those areas. The phylogenetic history of *Encopognathus* is, in all probability, rather similar to that outlined elsewhere for *Belomicrus*.

Tsaisuma,¹⁶ new subgenus

Lindenius Banks, Ann. Ent. Soc. Amer., XIV, p. 16 (1921). [Not of Lepeletier and Brullé, 1835.]

GENOTYPE: *Lindenius wenonah* Banks, 1921 [= *Encopognathus* (*Tsaisuma*) *wenonah* (Banks)].

The superficial habitus of *Tsaisuma* is very similar to that of *Rhectognathus*, from which it is readily distinguished by the thirteen-segmented

served in the Chirinda Forest of Southern Rhodesia " . . . tunnelling in a shady and sandy path. The prey is quite exceptional. Capt. Stevenson took a ♀ in the act of attacking an ant, *Tetramorium setuliferum* Em., and also dug out the contents of several galleries, consisting entirely of ants, but not all of the same species. Unfortunately the tube in which these specimens were preserved was accidentally destroyed, so that the identity of the several species cannot now be recorded."

¹¹ Arnold: Ann. Transvaal Mus., XI, p. 348 (1926).

¹² Cf. Pate: Trans. Amer. Ent. Soc., XLVI, pp. 254-255 (1940).

¹³ Cf. Pate: Trans. Amer. Ent. Soc. XLVI, pp. 252-253 (1940).

¹⁴ Timberlake: Ent. News, LI, p. 167 (1940).

¹⁵ Cf. Pate: Trans. Amer. Ent. Soc., XLVI, pp. 247-252, (1940).

¹⁶ After the Washo Indians of California, who were called the *Tsaisuma* by their neighbors, the northern Maidu.

antennae of the male, the foveolate mesonotal-scutellar suture, the patellate male fore tarsi, and the position of the antennal sockets, each of which is subcontiguous to the nearest lower inner orbit. In addition, the present phyletic strain of *Encopognathus* is unique in lacking basal acarid chambers on the abdominal tergites.

Diagnostic Features.—Compact, finely to subtilely punctate, small forms. Head subquadrate to suborbicular in anterior aspect, transversely subrectangular in dorsal aspect; inner orbits gently divergent above; posterior orbits simple, not bordered by a sharply marginate groove; malar space wanting. Vertex without supra-orbital foveae; ocelli situated in a low isosceles triangle; temples normal, ecarinate; occipital carina not a complete circle in extent nor attaining the hypostomal carinule bordering oral fossa. Antennae thirteen-segmented in males, twelve-segmented in females, situated low on face on dorsal margin of clypeus, the antenna sockets subcontiguous to nearest lower inner orbit and distinctly separated from each other. Mandible falcate; apices simple, acuminate; lower margin deeply excised medially.

Thorax robust. Pronotum situated on a level with mesonotum and without a complete transverse carinule anteriorly on dorsal surface. Mesonotum simple, hind angles not prominent; axillae small, not prominent, the lateral edges rounded, not margined nor reflexed; suture between mesonotum and scutellum impressed and foveolate. Mesopleura rounded anteriorly, without an epicnemium; episternal suture and mesopleural pit present and well developed; episternauli, mesopleurauli, hypersternauli, and sternauli all absent; mesothoracic epipleura not ankylosed with, but distinctly separated from mesopleura; mesepisterna without a vertical carina before middle coxae. Propodeum short, finely sculptured; dorsal face with a more or less distinct trigonal area basally; lateral carinae absent.

Wings in general as in *Rhectognathus*.

Fore legs of males with tarsi more or less patellate, and with a weak pecten. Middle tibiae with one small calcar apically; hind tibiae with two large apical calcaria.

Abdomen sessile; subfusiform, depressed. Tergites folded under roundly and imbricate with the flatly convex sternites. Tergites without apparent basal acarid chambers. Both sexes with a distinct pygidial area on ultimate tergite, that of male subtrapeziform, that of female trigonal. Males with apical sternites simple, unmodified.

Remarks.—In its finely punctate habitus, lack of basal acarid chambers on the abdominal tergites, and the full complement of thirteen segments in the antennae of the males, *Tsaïsuma* gives every indication of being the most generalized entity within the genus *Encopognathus*. Moreover, the simple immarginate axillae and unmodified hind mesonotal angles, the absence of supra-orbital foveae on the vertex and of a vertical carina before the middle coxae on the mesopleura, as well as the fact that the mesotho-

racic epipleura show no traces of ankylosis with the mesopleura are all evidence of an incontrovertible nature in support of the foregoing thesis. The present subgenus is evidently a representative of the ancestral and probably now extinct stock from which have arisen *Rhectognathus* and the two Old World phyletic strains: *Aryana* and *Encopognathus*.

Distribution.—The subgenus *Tsaisuma* is apparently a relict entity that has been isolated in western North America since the Miocene. In the Nearctic Region, its distribution on the eastern flanks of the Sierra Nevada coincides with that of its genotypic species, *wenonah*.

The Madrilene Spanish form, *Encopognathus braunsi*,¹⁷ may likewise be referable to *Tsaisuma*. This species I know solely through the medium of Mercet's¹⁷ and Kohl's¹⁸ descriptions, which indicate that *braunsi* is a finely punctate form lacking an epicnemium anteriorly and vertical carinae before the middle coxae on the mesopleura, and that the antennae of the males are thirteen-segmented. However, the position of the antennal sockets in relation to the inner orbits is not the same as in *wenonah*; moreover, the structural details of the abdomen, the legs of the males, and certain features of the head are unknown at present. Consequently, definite allocation of *braunsi* to *Tsaisuma* must await examination of authentic material of that species.

ENCOPOGNATHUS (TSAISUMA) WENONAH (Banks)

Figs. 7, 8, 13.

Lindenius wenonah Banks, Ann. Ent. Soc. Amer., XIV, p. 16, (1921); [♂].

The present species bears a superficial resemblance to *Encopognathus* (*Rhectognathus*) *pectinatus*, but in addition to the subgeneric features wherein it differs from that species, *wenonah* may be distinguished from *pectinatus* by the relatively simple non-pectinate thirteen-segmented antennae, the difference in livery, and the structure of the clypeus and middle tarsi, as well as the sculpture of the propodeum, all of which are described below.

Type.—♂; Tallac, El Dorado County, California. Elevation, 6000 feet. (W. M. Giffard.) [Museum of Comparative Zoölogy, Type no. 13819.]

Male. 4 mm. long. Black; the following stramineous: palpi, mandibles basally, clypeus, scape, pronotum dorsally to and including the tubercles. scutellum, postscutellum, axillary sclerites, abdominal tergites except the sides and a narrow testaceous caudal margin, all femora apically, and tibiae and tarsi entirely except in latter case the last two segments of fore and middle tarsi and last article of hind tarsi which are abruptly brunneous, as is also the outer apical angle of all fore tarsal segments and the outer laminate edge of patellate first segment. Pedicel and flagellum fulvous, the

¹⁷ *Encopognathus Braunsi* García Mercet, Bol. R. Soc. Españ. Hist. Nat., XV, pp. 367–370, figs. 1–3 (1915); [♂, ♀; SPAIN, Madrid Province: Madrid; Montarco; Aranjuez; Quadarrama].

¹⁸ Kohl: Ann. k. k. Naturhist. Hofmus. Wien, XXIX, pp. 320–321 (1915).

latter brunnescent apically. Abdomen light brunneous except for yellow maculations, and the deep fulvous last segment. Margin of clypeal lobe, and tegulae, fulvous-hyaline. Wings clear hyaline; veins and stigma fulvous.

Head subopaque; clypeus and front clothed with appressed silvery pile which is most noticeable on clypeus and lower inner orbits; temples more sparsely clad with puberulent silvery pubescence; vertex and upper portion of front with rather long, suberect setulae. Front with microscopically fine cancellate lineation upon which is superposed a series of moderate, rather close, setigerous punctures each bearing a suberect setula; bisected by a distinct longitudinal furrow running forward from median ocellus to a shallowly concave, glabrous, subnitidous, immarginate scapal basin between lower inner orbits. Vertex with surface sculpture and puncturation like that of front; ocelli situated in a low isosceles triangle, the postocellar distance one and eight-tenths the length of ocellocular line, the ocellar area bisected by a longitudinal furrow running back almost from median ocellus to occiput; no supra-orbital foveae. Temples with fine, moderate, separated punctures; temporal carinae absent; post-temporal region nitidous, glabrous. Antennae reaching about to tubercles, the sockets subcontiguous to nearest lower inner orbits, the interantennal distance four times the length of antennocular line; scapes straight, simple, ecarinate, obterete, three-sevenths (.43) in the vertical eye length; pedicel simple, orcate, one and one-third the length of first flagellar article; flagellum submoniliform, finely puberulent, first segment three-fourths the length of second, the first seven segments rounded out below as in figure, ultimate article simple, terete, one and six-tenths the length of penult segment. Clypeus transverse, subfusiform, median length two-sevenths (.286) the vertical eye length, flat laterally to tumid discally, produced medio-apically into a short, broad, subtruncate lobe, the apical margin of which is obscurely quadridentate. Mandibles slender, falcate; apices acuminate, simple; lower margins deeply excised medially.

Thorax subopaque; dorsum and prepectus clothed with short, decumbent, silvery pubescence. Pronotum short, transverse, linear, finely punctate, situated on a level with the mesonotum; dorsal surface deeply notched medially; anterior dorsal margin rounded medially but laterally on each side with a sharp transverse carinule which turns abruptly and descends vertically at each humeral angle. Mesonotum, scutellum and postscutellum with moderate close punctures; suture between mesonotum and scutellum deeply impressed and foveolate. Mesopleura fulgid, with moderately fine, well separated punctures, horizontally aciculate at level of strong mesopleural pit; anteriorly without an epicnemium; episternal suture distinct and strong; omauli, episternauli, mesopleurauli, hypersternauli, and sternauli all absent; metapleura fulgid, glabrous, subnitidous. Propodeum subfulgid; dorsal face glabrous, basally with a large subtriangular area with

many more or less irregular radiating carinules; posterior face discally with a broad cuneate, glabrous and nitidous, immarginate fovea, the lateral areas with sparse, decumbent, short silvery pubescence and traversed by fine, subparallel, horizontal rugulae.

Fore tarsi flattened, the first segment patellate, and provided with a weak pecten. Middle and hind tibiae with a few small weak spines on outer faces; middle tibiae with one small calcar apically, hind tibiae with two large distinct ones. Tarsi of middle and hind legs simple, normal.

Abdomen subfulgid; subfusiform, somewhat depressed; sparsely clothed with a fine appressed silvery puberulent pubescence, the third to last tergites with a scant vestiture of short suberect setulae; first to penult tergites with fine acupuncturation; ultimate tergite with an elongate subtrapeziform pygidium, the disc with a few well separated, very large and coarse, setigerous punctures each bearing a very short, decumbent light setula. Sternites flatly convex, with fine acupuncturation, and a scant vestiture of appressed puberulent pubescence.

Female. Unknown.

This distinctive little species is still known only from the unique male taken in the Lake Tahoe region of California.

Subgenus RHECTOGNATHUS Pate

Encopognathus (*Rhectognathus*) Pate, Ent. News, XLVII, p. 147 (1936).—Pate, Mem. Amer. Ent. Soc. no. 9, p. 56 (1937).—Timberlake, Ent. News, LI, p. 167 (1940).

GENOTYPE: *Encopognathus* (*Rhectognathus*) *pectinatus* Pate, 1936. (Monobasic and by original designation.)

Like *Tsaisuma*, the members of the present group are finely punctate New World forms with the mesopleura relatively simple, lacking both an epicnemium anteriorly and vertical carinae before the middle coxae; moreover, the vertex is devoid of supra-orbital foveae, the occipital carina is incomplete and does not attain the hypostomal carinule, while the pronotum is ecarinate, the axillae immarginate, the propodeum devoid of lateral carinae, and the abdomen is depressed. But unlike the preceding subgenus, *Rhectognathus* has the antennal sockets relatively remote from the lower inner orbits and the abdomen possesses distinct basal acarid chambers. Furthermore, the males of *Rhectognathus* have but twelve segments in the antennae, while the fore tarsi are not patellate as in *Tsaisuma*.

Diagnostic Features.—Small, compact, finely to subtilely punctate forms. Head orbicular in anterior aspect, transversely subrectangular in dorsal aspect; eyes naked, inner orbits gently divergent above; posterior orbits simple, not bordered by a sharply marginate groove; malar space wanting. Vertex without supra-orbital foveae; ocelli situated in a curved line; temples normal, ecarinate; occipital carina present but neither flanged, foveolate, a complete circle in extent, nor attaining hypostomal carinule bordering the oral fossa. Antennae twelve-segmented in both sexes, situated low

on face on dorsal margin of clypeus relatively remote from each other and also from nearest lower inner orbit. Mandibles falcate; apices simple, acuminate; lower margins deeply excised; inner margin bidentate medially. Females with a well developed psammophore consisting of mandibular, temporal, coxal, trochanteral, femoral and tibial ammochaetae.

Thorax robust. Pronotum situated on a level with mesonotum, the dorsal surface rounded, ecarinate. Mesonotum simple, hind angles not prominent; axillae small, not prominent, the lateral edges rounded, not margined nor reflexed; suture between mesonotum and scutellum not foveate; scutellum and postscutellum simple, their lateral edges immarginate. Mesopleura rounded anteriorly, without an epicnemium, and without a vertical carina before middle coxae; episternal suture and mesopleural pit present and well developed; episternauli, mesopleurauli, hypersternauli and sternauli all absent; mesothoracic epipleura and mesopleura not ankylosed but distinctly separated from each other. Propodeum short; finely sculptured; dorsal face with a more or less distinct trigonal area discally; lateral carinae absent.

Wings in general as in generic diagnosis.

Fore legs of females with the tibial and femoral ammochaetae present on both anterior and posterior margins, the tarsi flattened and with a pecten of short, stout spines; male fore tarsi simple or somewhat irregularly distorted but not patellate. Both sexes with one apical calcar on middle tibiae and two on hind tibiae.

Abdomen sessile; subfusiform, depressed. Tergites folded under roundly and imbricate with the convex sternites. Second to penult tergites with distinct basal acarid chambers. Second sternite simple, without impressed opaque oval spots; apical sternites of male simple, unmodified. Both sexes with a pygidial area on ultimate tergite.

Distribution.—The subgenus *Rhectognathus* is apparently a precinctive Nearctic entity closely related to, and obviously a derivative of, the immediate ancestral stock which gave rise to the preceding subgenus *Tsaissuma*. Two forms have been described which are referable to *Rhectognathus*: *pectinatus* and *rufiventris*. Both of these are known at present from only the southern portion of California. Eventually, however, the group will doubtless be found in the adjacent Great Basin and Colorado Plateau areas.

ENCOPOGNATHUS (RHECTOGNATHUS) PECTINATUS Pate

Figs. 3, 4, 5, 6, 9, 10, 12, 14.

Encopognathus (*Rhectognathus*) *pectinatus* Pate, Ent. News, XLVII, p. 148 (1936); [♂, ♀; Claremont and Bryson, California].—Timberlake, Ent. News, LI, p. 168 (1940); [♀; near Strathmore, Tulare Co., California].

The curious and characteristically formed twelve-segmented antennae and distorted fore tarsi distinguish *pectinatus* from the preceding form

wenonah. From *rufiventris*, which is as yet known only from a unique female, the corresponding sex of *pectinatus* may be differentiated by its septendentate clypeus and markedly different interantennal-antennocular ratio. Furthermore, in *rufiventris* the abdomen is largely ferruginous and the vertex and thorax, particularly the mesonotum and prepectus of the latter, are furnished with a fine basic cancellate to semi-aciculate sculpture which cause these areas to appear dull; in *pectinatus*, on the contrary, there is no such basic sculpture and the head and thorax are thus relatively fulgid, while the abdomen is largely black except for the entire last segment and the inflexed portion of the fourth and fifth tergites which are bright honey-yellow.

Type.—♂; Claremont, Los Angeles County, California. (C. F. Baker.) [Cornell University.]

Male. 5 mm. long. Black; the following eburneous; scapes entirely, pedicel and flagellum anteriorly and beneath save last article of latter which is wholly black, costa and subcosta of hind wing. The following stramineous: pronotal tubercles, postscutellum, fore femora with a stripe beneath, middle femora with a stripe anteriorly, all tibiae and tarsi. Abdomen with first two tergites black basally, remainder largely auranteous. Wings hyaline, tinged with fuscous; veins and stigma brunneous.

Head subfulgid; clypeus, except for glabrous disc, with appressed silvery sericeous pile; front, vertex and temples more thinly clad with short, decumbent to suberect, silvery pubescence. Inner orbits subparallel below, divergent above; front broad, very shallowly concave, discally with a glabrous, subnitidous but undelimited scapal basin, above with fine, separated, setigerous acupunctures and bisected by a weak furrow running forward from median ocellus; vertex tumid, punctate like front; ocelli moderate in size, situated in a curved line, the ocellocular line six-tenths the length of the postocellar distance; no channel or furrow from posterior ocelli to upper inner orbits; temples moderate, simple, ecarinate, finely but distinctly striatopunctate; occipital carina distinct but neither flanged, foveolate, a complete circle in extent, nor attaining the hypostomal carinule bordering the broad equilaterally trigonal oral fossa; post-temporal region more or less nitidous. Antennae as figured; scape three-sevenths (.43) the vertical eye length, ecarinate, strongly bowed, outer face strongly concave, narrow at base and quite wide just before apex; pedicel subequal in length to first flagellar article, flat beneath, outer distal angle with a long flabellate appendix; flagellum with first segment five-sixths the length of second and with outer distal angle produced into a moderately long dentoid process, second segment somewhat constricted at base, the distal article strongly compressed, the ultimate segment strongly flattened, subspatulate and five-fourths the length of penult article. Clypeus short, median length about one-fifth (.18) the vertical eye length, flat laterally to

gently tumid discally, produced medio-apically into a short, broad truncate lobe which is furnished with a flat, obliquely declivent, low isosceles trigonal, glabrous, nitidous bevel. Mandibles simple, acuminate at apex; lower margin deeply excised; inner margins bidentate medially.

Thorax more or less fulgid; clothed dorsally with a short, inconspicuous, aeneous pile; pleura and sterna with more noticeable, though thin, vestiture of decumbent silvery pubescence. Pronotum finely punctate, short, situated somewhat below level of mesonotum, anterior dorsal margin and lateral angles rounded, ecarinate, semicircularly notched medially above, laterad of notch with a shallow, transverse, concave furrow. Mesonotum lightly arched anteriorly, with fine, rather close, setigerous punctures throughout, anterior third with three parallel, widely separated, inconspicuous longitudinal lines; axillae small, simple, immarginate; suture between mesonotum and scutellum deeply impressed; scutellum flatly tumid, punctured like mesonotum, lateral edges immarginate; postscutellum tumid, subnitidous, arcuately margined anteriorly. Mesopleura finely acupunctate on prepectus, but becoming gradually subnitidous posteriorly; without an epicnemium anteriorly or carina or tubercle before middle coxae; episternal suture straight to slightly arched, and distinctly consute; mesopleural pit distinct; hind margin simple. Metapleura glabrous, nitidous. Mesosternum rounded anteriorly. Propodeum fulgid; posterior face with an inconspicuous vestiture of short, suberect silvery hairs, otherwise glabrous; dorsal face without a distinct trigonal enclosure, finely, irregularly areolate; posterior face discally with a large, submarginate, nitidous, oval fovea, laterad of which the surface is finely, irregularly reticulate; lateral carinae absent; lateral faces with fine, subparallel, horizontal rugulae and striae.

Legs, except tarsi, simple and relatively normal; middle and hind tibiae moderately spinose on outer faces; middle tibiae with a distinct apical calcar, hind tibiae with two calcaria. All metatarsi subequal in length to combined length of four distal segments. Fore tarsi with first segment strongly distorted, and on hind margin with a short row of stiff setae; middle tarsi with metatarsi strongly arcuate; hind metatarsi constricted at base, thickened at apex, at base below with a row of slender spinules and stiff setulae.

Abdomen subfulgid; depressed; subobcordate; with a thin vestiture of short, decumbent hairs. Tergites and sternites with fine, well separated acupunctures; first tergite with a strong longitudinal impression bisecting basal half; second to penult tergites with distinct basal acarid chambers; last tergite with a trapeziform pygidial area, truncate at apex, the disc with scattered, coarse punctures each bearing a short decumbent seta. Sternites flatly convex, with microscopically fine cancellate sculpture upon which is superposed on second sternite a series of scattered acupunctures; apical sternites relatively simple, without tubercles or processes; hind

margin of sixth entire, of seventh broadly emarginate; hypopygium oblong convex, finely and closely acupunctate, apex truncate with distolateral angles rounded.

Allotype.—♀; Claremont, Los Angeles County, California. (C. F. Baker.) [Cornell University.]

Female. 6.5 mm. long. Agrees with the male (type) in all essential features of livery and structure except as follows:

Livery: The following stramineous: pronotum dorsally with a stripe on each side of median excision, tegulae anteriorly, axillary sclerites, costa and subcosta of hind wing, fourth abdominal tergite with a narrow, indistinct preapical fascia, fifth tergite with a broader preapical fascia, last abdominal segment entirely, inflexed portions of fourth and fifth tergites and portions of some of preceding tergites also, fore femora entirely save posterior basal half. Dark castaneous: mandibles medially, trigonal clypeal bevel and platform, pedicel and flagellum above.

Head without an oblique channel or furrow from posterior ocelli to upper inner orbits. Antennocular distance about three-sevenths (.44) the interantennal line. Antennae relatively simple; scape subcylindrical, ecarinate, very slightly bowed, and one-half the vertical eye length; pedicel depressed, otherwise simple, subequal in length to first flagellar article; flagellum simple, finely puberulent, first segment one and a half times the length of second segment, ultimate article simple, terete, one and a half times the length of penult segment. Clypeus about one-fourth (.22) the vertical eye length; flat laterally to strongly tumid discally where it is elevated into a trigonal, glabrous, nitidous, slightly concave, obliquely declivent platform terminating in a short, broad median lobe which is septendentate.

Psammophore well developed and composed of the following series of ammochaetae: mandibular (on both inner and lower margins), temporal, coxal, trochanteral, femoral and tibial (the femora and tibiae with a set on both anterior and posterior margins).

Thorax in general as in male but scutellum finely, longitudinally striatopunctate. Propodeum with dorsal face with transverse, parallel, slightly arcuate, rugulae; posterior face with discal fovea more indistinct, and opaque within.

Legs relatively simple. Fore tarsi strongly flattened and with a distinct pecten of elongated, flattened and flexible bristles. Outer faces of middle and hind tibiae moderately spinose; middle tibiae with one calcar, hind tibiae with two.

Abdomen as in male, but last tergite with an equilaterally trigonal, flat pygidial area, the disc of which has coarse, scattered punctures, each bearing a short decumbent seta.

Variation.—In the series of specimens studied, there is relatively little structural disparity from the typical pair other than minor variations in

the intensity of the propodeal sculpture. The median clypeal tooth in the female from the Gavilan is very indistinct, but this specimen otherwise agrees in all essential structural details with the allotype of *pectinatus*. The livery is much the same in all the material examined, save that the specimens from the Gavilan are inclined to be somewhat melanic.

Specimens examined: 8; 5 males, 3 females, as follows:

CALIFORNIA: Bryson, Monterey County; April 23, 1917; (E. P. Van Duzee); 3 ♂; [paratypes; Cornell]. Near Strathmore, Tulare County; March 29, 1937; (P. H. Timberlake; at flowers of *Baeria chrysostoma*); 1 ♀; [Timberlake]. Claremont, Los Angeles County; (C. F. Baker); 1 ♂, 1 ♀; [type and allotype; Cornell]. Gavilan,¹⁹ Riverside County; April 10, 1940; (P. H. Timberlake; at flowers of *Baeria gracilis*); 1 ♂: April 18, 1940; (P. H. Timberlake); 1 ♀; [Timberlake].

Distribution.—The range of *pectinatus* extends from the Coast Ranges of Monterey County and the foothills of the Sierra Nevada in central Tulare County southward, presumably skirting the Mohave Desert where *rufiventris* occurs, well into the piedmont of the Transverse Ranges district in Los Angeles and Riversides Counties. From the present records, it would appear that *pectinatus* is chiefly an early vernal form, unless, of course, as may very well happen, more than one generation a year of this species occurs.

ENCOPOGNATHUS (RHECTOGNATHUS) RUFIVENTRIS Timberlake

Figs. 11, 15.

Encopognathus (Rhectognathus) rufiventris Timberlake, Ent. News, LI, p. 167 (1940); [♀].

The bright ferruginous abdomen, more opaque habitus, sexdentate clypeal lobe, the oblique arcuate furrow running from the posterior ocelli to the upper inner orbitis, and the subequal antennocular and interantennal distances immediately distinguish *rufiventris* from the female sex of *pectinatus*.

Type.—♀; Ten miles southwest of Victorville, San Bernardino County, California. May 6, 1939. (P. H. Timberlake; at flowers at *Phacelia distans* [Wild Heliotrope].) [Citrus Experiment Station, Riverside.]

Female.—5 mm. long. Black; the following eburneous: scape entirely, pedicel beneath, basal segments of flagellum beneath, pronotal tubercles, postscutellum, all femora at apex, tibiae save for an elongate brunneous spot on inner faces, fore tarsi and middle and hind metatarsi. Mandibles dark miniatous at base and apex, dark castaneous medially. Tegulae and axillary sclerites testaceous, the former with an eburneous spot anteriorly on disc, the latter with outer margins eburneous. Abdomen bright ferruginous except for the following which are black or dark brunneous: basal two-thirds of first tergite, a large transverse oval spot anteriorly on disc of second, third and fourth tergites, and venter largely except last segment;

¹⁹ This is a plateau region, known locally as "The Gavilan" or "El Gavilan," between Gavilan Peak and the Cajalco Reservoir to the north of it.

apical margins of second to fifth sternites broadly testaceous. Wings hyaline, slightly infumated; stigma and veins dark brunneous.

Head subopaque; clypeus, except for nitidous discal platform, and lower inner orbits with a heavy, appressed, silvery sericeous pile; vertex and upper portion of front thinly clad with short, erect, light aeneous hair. Inner orbits divergent above; front relatively flat and finely punctate, the disc of anterior face with a shallow, concave, glabrous and nitidous, undefined scapal basin; vertex and upper portion of front with a microscopically fine cancellate sculpture upon which is superposed a series of moderately close, setigerous, acupunctures; ocelli situated in a curved line, the ocellular distance a little less than half (.46875) the length of postocellar line, from outer margins of each posterior ocellus an arcuate furrow curves obliquely forward to upper inner orbits, and from anterior ocellus a weak furrow bisects upper portion of front; temples strongly striatopunctate; post-temporal region glabrous, nitidous; occipital carina distinct but neither flanged, foveolate, a complete circle in extent nor attaining the hypostomal carinule bounding the broad trigonal oral fossa. Antennae with scape ecarinate, subcylindrical, very slightly bowed, and about half (.53) the vertical eye length; pedicel simple, obterete, slightly flattened beneath, four-fifths the length of first flagellar article; flagellum simple, finely puberulent, first segment five-sixths the length of second which is one and a half times the length of the third, last article simple, terete, and one and a half times the length of the penult segment. Clypeus short, median length about one-quarter (.235) the vertical eye length; flat laterally, elevated discally into a short, broad, rounded keel which terminates in a glabrous and nitidous, obliquely declivent, flat isosceles trigonal platform, the apical margin of which is sexdentate. Mandibles with apices simple, acuminate, lower margins strongly excised; inner margins bidentate medially.

Psammophore very well developed; with the same series of ammochætae as in *pectinatus*.

Thorax subopaque to subfulgid; dorsally with a very thin and scanty vestiture of erect, light puberulent hairs; pleura with more noticeable decumbent silvery pubescence. Pronotum very short, situated somewhat below the level of arched mesonotum; dorsal surface ecarinate, inconspicuously notched medially, traversed by a very narrow furrow; sculptured like mesonotum. Mesonotum with a microscopically fine longitudinal semi-aciculate to substriatopunctate type of sculpture upon which is superposed a series of moderately fine, irregularly scattered, setigerous punctures; anterior half bisected by a fine double longitudinal line, laterad of which the notauli are indicated; parapsidal furrows indicated on each side by a sharp, nitidous, cuneate impression; axillae simple, moderate, immarginate; suture between mesonotum and scutellum very deeply impressed, ter-

minating laterally on each side in a small trigonal fovea; scutellum flatly tumid, longitudinally semi-aciculate and with sparse, irregularly scattered punctures, lateral edges immarginate; postscutellum tumid, finely and sparsely acupunctate, arcuately margined anteriorly. Mesopleura anteriorly with sculpture and puncturation like vertex, becoming gradually subnitidous posteriorly; anteriorly without an epicnemium and without carinae or tubercles before middle coxae; episternal suture straight, finely consute; metapleural pit distinct; posterior margin finely subconsute; metapleura glabrous, nitidous, hind margin foveolate below; mesosternum rounded, ecarinate anteriorly. Propodeum short, subopaque, with a thin vestiture of short, suberect, silvery hairs on posterior face, otherwise glabrous; dorsal face traversed anteriorly by fine rugulae radiating from anterior margin, and posteriorly by transverse parallel arcuate rugulae, all of which are connected by minute rugulae to form a series of small, irregular areoles, a large, poorly delimited trigonal enclosure present, the apex terminating in the moderately large, submarginate trigonal discal fovea of posterior face, the fovea fulgid and rugulate within, the lateral surfaces finely, irregularly, clathrately rugulose; lateral carinae wanting; lateral faces with parallel horizontal rugulae.

Legs with fore tarsi flattened and provided with a distinct pecten of elongate, flattened and somewhat flexible bristles. Middle and hind tibiae moderately spinose on outer faces; middle tibiae with one apical calcar, hind tibiae with two calcaria.

Abdomen fulgid; depressed, subcordiform; with microscopically fine cancellate sculpture upon which is superposed on tergites and second and last sternites a series of well separated, setigerous acupunctures; sternites with a subapical transverse row of setigerous punctures; ultimate tergite with a flat, equilaterally trigonal pygidial area, the disc with scattered coarse punctures each bearing a short decumbent seta.

Male. Unknown.

This late vernal to early aestival form of California's Mohave Desert is still known from only the unique female recorded above.

Aryana,²⁰ new subgenus

Oxybelus [not of Latreille]: Cameron, Mem. & Proc. Manchester Lit. & Phil. Soc. (4), III, pp 276, 280, (1890).—Dalla Torre, Cat. Hymen., VIII, p. 638 (1897).

Crabro [in part]: Bingham, Fauna Brit. Ind., Hymen., I, pp. 322, 328 (1897).—Schulz, Spolia Hymen., p. 210 (1906).—Pate, Philippine Journ. Sci., LXIV, p. 388 (1938).

Crabro (Artengruppe *Encopognathus*) Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XXIX, p. 320 (1915).

GENOTYPE: *Encopognathus* (*Aryana*) *oxybeloides* new species.

The presence of supra-orbital foveae on the vertex, of a distinct epicnemium anteriorly and vertical carinae before the middle coxae on the

²⁰ After the *Arya*, one of the early peoples of India.

mesopleura, and of well developed lateral carinae on the propodeum, as well as the coarsely punctate habitus, the occipital carina reaching the hypostomal carinule, the strong and transversely carinate pronotum, the sharply margined lateral axillar edges, the non-depressed abdomen, and the lack of a psammophore in the female sex, all attest the close affinity *Aryana* bears to the nominate group. However, in *Encopognathus* in the restricted sense, the pleura and epipleura of the mesothorax are ankylosed, the posterior orbits are bordered by a sharply marginate groove, the antennal sockets are subcontiguous to the nearest lower inner orbit and the males have but twelve antennal articles, whereas conversely in *Aryana* the mesopleura are distinctly separated from the epipleura and the posterior orbits are simple and immarginate as they are in the New World entities *Rhectognathus* and *Tsaisuma*, while like *Rhectognathus* the antennal sockets are relatively remote from the lower inner orbits, and the males have thirteen-segmented antennae as in *Tsaisuma*.

From the other three subgenera of *Encopognathus* the members of *Aryana* are distinguishable from, and unique in possessing distinct and well developed mesopleural hypersternauli, an impressed, oblique, opaque ovate spot laterally on each side of the second abdominal sternite, and in the following venational features: the transverse cubital vein of the fore wing is oblique and somewhat sinuate instead of being distinctly angulate medially, while the submedian cell of the hind wing is quite long with the anal lobe but half its length, in sharp contradistinction to the condition found in *Tsaisuma*, *Rhectognathus* and *Encopognathus*, all of which have the submedian cell relatively short with the anal lobe subequal in length to it.

Diagnostic Features.—Small, compact, robust, coarsely punctate forms with a superficial habitus much like that of the genus *Oxybelus*. Head sub-orbicular in anterior aspect, transversely subrectangular in dorsal aspect; eyes naked, more coarsely faceted anteriorly than posteriorly; inner orbits strongly arcuate, divergent above and below much as in *Anacrabro*; posterior orbits not bordered by a marginate groove; malar space wanting. Vertex with well developed supra-orbital foveae; ocelli situated in a low isosceles triangle; temples normal, often with temporal carinae present; occipital carina attaining hypostomal carinule bordering oral fossa. Antennae situated low on face on dorsal margin of clypeus; thirteen-segmented in males,²¹ twelve-segmented in females, the interantennal and antennoocular distances subequal. Mandibles falcate, apices simple, acuminate, lower margin with a strong excision medially. Females without a psammophore.

Thorax robust. Pronotum short, transverse, linear, anterior dorsal margin transversely carinate, situate on a level with the mesonotum. Mesonotum with hind angles acute or produced into a spinoid tooth;

²¹ An assumption based on the statements of Kohl (1915, Ann. k. k. Naturhist. Hofmus. Wien, XXIX, p. 320). I have seen no males of this group.

axillae relatively large, lateral edges sharply margined or reflexed; suture between mesonotum and scutellum more or less impressed and foveolate; scutellum with lateral edges simple, not sharply margined or reflexed; post-scutellum simple, unarmed. Mesopleura with a sharp epicnemium anteriorly, and before middle coxae with a vertical carina; mesothoracic epipleura distinctly separated from mesopleura; episternal suture distinct and well developed; hypersternauli present; mesopleural pit distinct; episternauli absent. Propodeum very short; more or less coarsely sculptured or areolate; dorsal face with a more or less distinct trigonal area basally; posterior face vertical, with a discal areole or fovea; lateral carinae present, well developed.

Fore wings with transverse cubital vein oblique, slightly sinuate; hind wings with submedian cell elongate, the anal lobe only about one-half its length. Wings otherwise as in *Encopognathus*.

Legs stout. Middle and hind legs with outer faces of tibiae provided with many short stout peg-like spines; middle tibiae with one apical calcar, hind tibiae with two. Fore tarsi of females somewhat flattened and with a pecten.

Abdomen sessile; fusiform, but not depressed. Second to penult tergite with basal acarid chambers, and folded under roundly and imbricate with the convex sternites. Second sternite laterally on each side with an impressed, oblique, opaque, ovate spot. Ultimate tergite of both sexes with a distinct pygidial area.

Component Species.—The subgenus *Aryana* has been erected primarily for the reception of the following peculiar and distinctive new form, *Encopognathus oxybeloides*. But it also includes in all probability the Indian species *bellulus*,²² which Cameron originally described as an *Oxybelus*, and the undescribed species Kohl recorded from Deesa.²³ Moreover, it is not unlikely that when a critical study is made of the types of the many Indian Pemphilids described during the past half century, and merely assigned to the blanket genus *Crabro*, one or more of them may prove to be referable to *Aryana*.

Distribution.—The subgenus *Aryana* is known at present from only the Indian province of the Oriental Region where one species occurs in the Northwestern States, another in the Bombay Presidency, while a third is found on the Coromandel Coast. Eventually, however, *Arayana* will doubtless be found ranging throughout peninsular India, and also in all

²² *Oxybelus bellus* Cameron, Mem. & Proc. Manchester Lit. & Phil. Soc. (4), III, pp. 276, 280 (1890), (*nec* Dahlbom, 1845); [♂; Poona, Bombay Presidency, India].—*Oxybelus bellulus* Dalla Torre, Cat. Hymen., VIII, p. 638 (1897); [new name for *O. bellus* Cameron, 1890, *nec* Dahlbom, 1845].—*Crabro bellus* Bingham, Faun. Brit. Ind., Hymen., I, p. 328 (1897); (*nec* Cresson, 1865); [♂; Poona, India].—*Crabro bellulus* Schulz, Spolia Hymen., p. 210 (1906); Pate, Philippine Journ. Sci., LXIV, p. 388, (1938).

²³ Kohl: Ann. k. k. Naturhist. Hofmus. Wien, XXIX, p. 320 (1915).

probability in at least the eastern portion of the Eremian province of the Palaearctic Region.

Encopognathus (Aryana) oxybeloides,²⁴ new species

Figs. 1, 2.

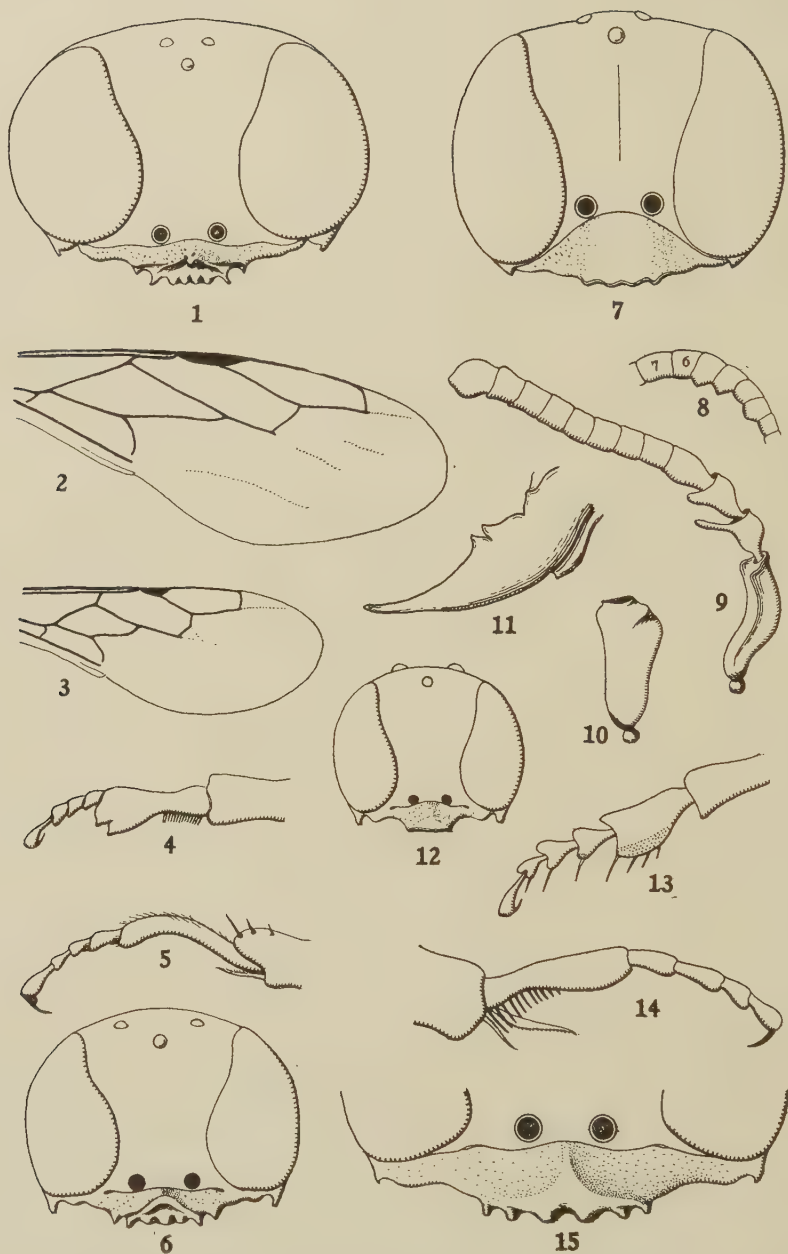
The present species is apparently closely allied to *bellulus* (Dalla Torre), but may be readily differentiated from that form of the Western Ghats by its ecarinate mesonotum, yellow scutellum and black mesopleura.

Type.—♀; Nedungadu, Tanjore, Madras Presidency, India. May 19. [Museum of Comparative Zoölogy, Harvard College.]

Female.—8 mm. long. Black; the following citrinous: mandibles except red apices, pronotum dorsally to and including the tubercles, scutellum, postscutellum, prepectus, tegulae with a discal spot, axillary sclerites along outer margins, first five abdominal tergites with large quadrate spots laterally, fore and middle legs entirely save upper bases of femora, and hind legs with coxae, trochanters, tibiae and tarsi entirely and femora broadly annulate at base. Tegulae and axillary sclerites light brunneous save for yellow maculations. Wings hyaline, iridescent; stigma and veins light brunneous.

Head more or less fulgid; inner orbits broadly, and clypeus save for the bevel, with a heavy vestiture of appressed silvery sericeous pile; vertex with a sparse clothing of suberect, aeneous, puberulent pubescence; temples clad with appressed silvery hairs. Inner orbits arcuate, gently divergent above and below; front broad, flatly concave, medially with an elongate, glabrous, nitidous area, medially above with a small pit-like fovea, raised slightly along inner orbits. Vertex with rather coarse, close punctures; supra-orbital foveae very distinct, parallel to upper inner orbits, elongate-linear and surrounded by a narrow, glabrous, nitidous welt; ocelli situated in a curved line, the median ocellus placed in a shallow concave basin, post-cellular line twice the ocellocular distance; temples normal, closely striato-punctate, temporal carinae present, sharp and distinct for entire length; occipital carina complete, reaching hypostomal carinule bordering oral fossa some distance from midventral line of head. Antennae with sockets remote from each other and from nearest lower inner orbit, the inter-antennal distance five-fourths the length of antennocular line; scapes straight, slightly obterete, ecarinate, three-fifths the vertical eye length; pedicel suborcate, two-thirds the length of first flagellar article; flagellum simple, finely puberulent, first segment one and a half times the length of second which is six-fifths the length of third, ultimate article simple, terete, about twice the length of penult sement. Clypeus short, transverse, median length one-fifth the vertical eye length; flat and attenuate laterally to

²⁴ In allusion to its pronounced, though superficial, resemblance to members of the genus *Oxybelus*.



Encopognathus (Aryana) oxybeloides new species; female (type: Nedungadu, Tanjore, India): Fig. 1.—Anterior aspect of head. Fig. 2.—Fore wing.

Encopognathus (Rhectognathus) pectinatus Pate; male (type: Claremont, California): Fig. 3.—Fore wing. Fig. 4.—Fore tarsus, oblique aspect. Fig. 5.—Middle tarsus, lateral aspect. Fig. 9.—Antenna. Fig. 10.—Lateral aspect of scape. Fig. 12.—Anterior aspect of head. Fig. 14.—Hind

tumid and subtuberculate discally, medio-apically with a declivent, glabrous and nitidous, low subtrigonal bevel, the apical margin of which is notched medially, sinuate laterally to a sharp dentiform angle then bi-emarginate with two further lateral teeth. Mandibles falcate; apices simple, acuminate; lower margins deeply excised medially; inner margins medially with a low obtuse dentiform angle. Psammophore undeveloped.

Thorax robust; fulgid; with a moderately coarse and close puncturation throughout; dorsally with a thin vestiture of decumbent light aeneous hair; pleura and sterna with similar clothing of silvery pubescence. Pronotum short, transverse, linear, anterior dorsal margin sharply and transversely carinate to and including the tubercles, the carinule briefly interrupted at the sharply angulate humeral angles. Mesonotum with hind angles produced into a short, nitidous, acuminate spinoid tooth; axillae large, ovate, flat, lateral edges sharply margined; scutellum with fore and hind margins impressed and consute, the lateral margins simple, not sharply edged; post-scutellum simple, impunctate. Mesopleura anteriorly with a sharp epicnemium continued ventrocaudad on each side to the strong vertical carina before middle coxae; mesopleural pit, hypersternauli and episternal suture all distinct, the last two more or less consute; metapleura punctured like mesopleura; mesosternum rounded anteriorly, not transversely margined. Propodeum, except for disc of dorsal face, with a thin vestiture of short, suberect, light pubescence; dorsal and posterior face irregularly areolate, the former more distinctly so, the latter with an indistinct lyriform enclosure discally; lateral carinae well developed for entire length; lateral faces with fine subparallel horizontal carinules.

Fore wing with marginal cell narrow, elongate, five times as long as broad, and broadly, obliquely truncate at apex; transverse cubital vein oblique, arcuate, joining radius about its middle; recurrent vein joining cubitus about two-thirds the way from its base. Hind wing with the anal lobe but one-half the length of the narrow, elongate submedian cell.

Legs stout; fore metatarsi of females flattened and with a pecten of short stiff spines. Outer faces of middle and hind tibiae with many short to elongate, stout peg-like spines; middle tibiae with one calcar, hind tibiae with two apical calcaria.

Abdomen fulgid; rather coarsely punctate throughout; constricted somewhat between the segments; with a moderate vestiture of decumbent silvery pubescence. Second to penult tergites with distinct basal acarid chambers; ultimate tergite with a cordate pygidium very densely clothed

tarsus, lateral aspect. Female (allotype; Claremont, California): Fig. 6.—Anterior aspect of head.

Encopognathus (Tsaisuma) wenonah (Banks); male (type; Tallac, California): Fig. 7.—Anterior aspect of head. Fig. 8.—First seven segments of flagellum. Fig. 13.—Fore tarsus.

Encopognathus (Rhectognathus) rufiventris Timberlake; female (type: 10 miles southwest of Victorville, California): Fig. 11.—Mandible. Fig. 15.—Anterior aspect of clypeal region.

with appressed aeneous hair. Second sternite with an oblique, concave, opaque, oval spot laterally on each side.

Male.—Unknown.

Only the unique female, described above, of this interesting species from the Coromandel Coast is known.

Subgenus ENCOPOGNATHUS Kohl

Crabro (Haupt-Artengruppe *Lindenius*: Artengruppe *Encopognathus*) Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XI, p. 486 (1896).—Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XXIX, p. 320 (1915).

Thyreopus (species-group *Encopognathus*) Arnold, Ann. Transvaal Mus., XI, p. 346 (1926).—Arnold, Occ. Pap. Rhodesian Mus., no. 1, p. 17 (1932).—Arnold, Check List Sphegid, Ethiop. Reg., p. 13 (1930).

Encopognathus Ashmead, Canad. Entom., XXXI, p. 166 (1899).—Turner, Ann. & Mag. Nat. Hist. (8), IX, p. 419 (1912).—Turner, Ann. & Mag. Nat. Hist. (8), XIX, p. 106 (1917).

Encopognathus (*Encopognathus*) Pate, Ent. News, XLVII, p. 147 (1936).—Pate, Mem. Amer. Ent. Soc., no. 9, p. 25 (1937).

GENOTYPE: *Crabro* (*Encopognathus*) *Braueri* Kohl, 1896 [= *Encopognathus* (*Encopognathus*) *braueri* (Kohl)]. (Monobasic.)

As here understood, *Encopognathus*, in the restricted sense, comprises an aggregation of coarsely punctate African forms, distinguished from all the preceding subgenera in having the mesothoracic epipleura ankylosed with the mesopleura and the posterior orbits bordered by a sharply marginate groove. The remaining characteristics differentiating the present group from the other three entities have been presented on a preceding page in the key to subgenera and also in the introductory discussion under *Aryana*.

Diagnostic Features.—More or less compact, coarsely punctate, small forms. Head suborbicular to subquadrate in anterior aspect, transversely subrectangular in dorsal aspect; eye naked, more coarsely faceted anteriorly than posteriorly; inner orbits convergent toward clypeus; posterior orbits bordered by a sharply marginate groove; malar space wanting. Vertex with well developed supra-orbital foveae; ocelli situated in a low isosceles triangle; temples somewhat abbreviate; occipital carina attaining the hypostomal carinule bordering the oral fossa some distance from mid-ventral line of head. Antennae twelve-segmented in both sexes, situated low on face on dorsal margin of clypeus, the sockets well separated from each other but subcontiguous to nearest lower inner orbit, scapes more or less cylindrical, ecarinate. Mandibles more or less falcate; apices simple, acuminate; lower margins distinctly excised. Females without a psammophore.

Thorax robust. Pronotum short, transverse, anterior dorsal surface transversely carinate for its entire width, and situated on a level with the mesonotum. Mesonotum with hind angles acute; axillae large, flat, with a sharply margined or reflexed lateral edge; scutellum with lateral margins

reflexed or sharply margined; postscutellum simple, or the lateral and posterior margins with processes or alate expansions. Mesopleura with a sharp epicnemium anteriorly and vertical carinae before middle coxae; mesothoracic epipleura more or less indistinguishably ankylosed with mesopleura; mesopleural pit present but somewhat obscured by the coarse sculpture; episternauli, mesopleurauli, hypersternauli, and sternauli all absent. Propodeum short; more or less coarsely areolate or sculptured; dorsal face with a more or less distinct trigonal area basally; lateral carinae present and well developed.

Legs relatively stout. Middle and hind tibiae with outer faces more or less strongly spinose; middle tibiae with one apical calcar, hind tibiae with two calcaria. Females with a pecten on fore tarsi.

Fore and hind wings as in generic diagnosis.

Abdomen sessile; compactly fusiform to elongate; more or less coarsely punctate. Tergites folded under roundly and imbricate with the convex sternites, the second of which in the female sex lacks a small ovate opaque spot laterally on each side. Second to penult tergites with basal acarid chambers. Ultimate tergite with a distinct pygidial area in both sexes.

Remarks.—The coarsely punctate habitus, the ankylosed pleura and epipleura of the mesothorax, the reduced number of segments in the antennal flagellum of the males, and the frequently armed or appendiculate postscutellum indicate that the nominate complex indubitably represents the most highly evolved and specialized group within the genus *Encopognathus*.

Component Species.—The build of the six species that may be referred to the nominate subgenus is quite diversified. On the basis of the structure of the postscutellum and the shape of the abdomen, these forms are roughly divisible into two distinct groups of species: The Braueri Group, comprising *braueri*,²⁵ *rugosopunctatus*,²⁶ and *rhodesianus*,²⁷ all of which have the postscutellum simple and unarmed, and the abdomen relatively short and compact; and the Brownei Group, consisting of *brownei*,²⁸ *granulatus*,²⁹ and

²⁵ *Crabro* (*Encopognathus*) *Braueri* Kohl, Ann. k. k. Naturhist. Hofmus. Wien, XI, p. 486, text-fig. 89 (1896); [♀ (?); Senegambia].—*T[hyreopus]* (*Encopognathus*) *Braueri* Arnold, Ann. Transvaal Mus., XI, p. 346, (1926).

²⁶ *Encopognathus rugosopunctatus* Turner, Ann. & Mag. Nat. Hist. (8), IX, p. 419 (1912); [♀; NATAL: Durban].—*T[hyreopus]* (*Encopognathus*) *rugosopunctatus* Arnold, Ann. Transvaal Mus., XI, p. 345 (1926).

²⁷ *T[hyreopus]* (*Encopognathus*) *rhodesianus* Arnold, Occ. Pap. Rhodesian Mus., no. 1, p. 19, figs. 10, 10a (1932); [♀, ♂; SOUTHERN RHODESIA: Spongweni].

²⁸ *Encopognathus Brownei* Turner, Ann. & Mag. Nat. Hist. (8), XIX, p. 106 (1917); [♀; BRITISH EAST AFRICA: Tana River, 3000 feet, near Mt. Kenia].—*T[hyreopus]* (*Encopognathus*) *Brownei* Arnold, Ann. Transvaal Mus., XI, p. 346 (1926).—*T[hyreopus]* (*Encopognathus*) *egregius* Arnold, Ann. Transvaal Mus., XI, p. 347, figs. 4a, 4b (1926); [♀; SOUTHERN RHODESIA: Sawmills; Rhodesdale (nesting in sandy banks)].—*T[hyreopus]* (*Encopognathus*) *Brownei* Arnold, Ann. Transvaal Mus., XII, p. 122 (1927); [*egregius* Arnold placed as a synonym of *brownei* Turner].

chirindensis,³⁰ in which the abdomen is more or less elongate and the post-scutellum armed,—in the case of the first two species with a pellucid translucent laminate lamella around the posterior and lateral margins, while the last, *chirindensis*, has the postscutellum bilobate and produced backward on each side in the form of a trigonal, thick, opaque laminate plate.

The admirable papers of Arnold³¹ may be consulted for detailed descriptions and figures of the foregoing six species.

Distribution.—The nominate subgenus of *Encopognathus* is apparently confined wholly to the Ethiopian Region. Of the six species now known, one (*braueri*) inhabits Senegambia, another (*granulatus*) has been recorded only from the eastern area of the Lower Guinea Forest District in the Belgian Congo, a third (*rugosopunctatus*) is known at present only from Natal, while the remaining three (*brownei*, *rhodesianus*, and *chirindensis*) are relatively common and have been taken at a number of localities in Southern Rhodesia.

I have seen two females of *E. brownei* from the Sanyati Valley, Southern Rhodesia, taken September–October, 1925.

²⁹ *T[hyreopus]* (*Encopognathus*) *granulatus* Arnold, Ann. Transvaal Mus., XI, p. 348 (1926); [♀; BELGIAN CONGO: Penge].

³⁰ *T[hyreopus]* (*Encopognathus*) *chirindensis* Arnold, Occ. Pap. Rhodesian Mus., no. 1, p. 17, figs. 11, 11a, 11b (1932); [♂, ♀; SOUTHERN RHODESIA: Chirinda Forest (tunnelling in a shady and sandy path)].

I have seen the following material of *E. chirindensis*: SOUTHERN RHODESIA: Chirinda Forest, May 1930, 1 ♂ (paratype). Mt. Selinda, November–December, 1930, 1 ♂, 1 ♀.

³¹ Arnold: Ann. Transvaal Mus., XI, pp. 345–349 (1926).—Occ. Pap. Rhodesian Mus., no. 1, pp. 17–20 (1932).